Systematics, biogeography and morphological evolution in *Entosthodon* Schwägr. (Bryopsida, Funariaceae) with a revision of the genus in Africa

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Abstract

Entosthodon Schwägr. (Funariaceae) is a genus of soil-inhabiting, annual to biennial mosses occurring worldwide in temperate to tropical-montane climates. Although a number of regional revisions and treatments exist for the genus, in many parts of the world, it remains poorly known. This is perhaps especially true in Africa, where the identities of most species names are obscure. Furthermore, recent work on the Funariaceae suggests that the sporophytes, long used as the main basis for classification and identification in the group, exhibit high levels of homoplasy and that *Entosthodon* is paraphyletic as currently circumscribed. I further test the monophyly of *Entosthodon*, and its relationships to other members of the Funarioideae, through phylogenetic analysis of DNA sequences from four chloroplast regions. These analyses included 45 *Entosthodon* species (*ca*. 50 % of those currently recognised), as well as an additional 22 species comprising representatives of all genera of the subfamily (except the rare, monotypic genera *Cygnicollum, Clavitheca, Nanomitrella* and *Brachymeniopsis* and the recently described monotypic *Afoninia*). Bayesian analyses of these data strongly contradict the monophyly of *Entosthodon*, and it is instead resolved as paraphyletic to a large clade comprising mostly members of *Physcomitrium* and *Physcomitrella*. Within this grade, five well supported lineages are resolved – the first comprises 3 species of *Entosthodon* and is sister to the second lineage, the monotypic *Physcomitrellopsis*. The third is sister to the aforementioned

clades and comprises 11 species of *Entosthodon* within which the monotypic genus *Funariella* is embedded. The fourth lineage comprises 7 species of *Entosthodon* and is sister to a clade within which a *Physcomitrium-Physcomitrella* group is sister to the fifth lineage - a large clade comprising 24 species of *Entosthodon*. *Entosthodon hungaricus* is shown to belong in the Physcomitrium clade instead, consistent with its rostrate operculum. Based on the phylogeny, a new classification of *Entosthodon sensu lato* is proposed. The genus is split into 4 genera (*Amphoritheca, Fifeobryum gen nov.*, *Funariella* and *Entosthodon sens. str*.) and the monophyletic *Physcomitrellopsis* is also maintained. Because of a lack of diagnostic morphological taxonomic characters this new classification is based largely on the molecular circumscription of clades. Nonetheless, particular character combinations do largely characterise most of these genera, albeit that frequent reversals render particular character states non-diagnostic. A revision of these five genera for Africa results in the recognition of twenty-six species in total: three in *Amphoritheca*, 12 in *Entosthodon*, one in *Physcomitrellopsis*, one in *Fifeobryum*, and nine in *Funariella*. Six of these species, 4 in *Entosthodon* and 2 in *Funariella*, are newly described based on specimens from East and southern Africa. A key to the sub-Saharan species is provided, and each is fully described, mapped and illustrated. To better understand the global diversification of the three main *Entosthodon* lineages, ancestral area and climatic niche were reconstructed in a temporal setting. Divergence time estimates place the origins of the main lineages of *Entosthodon s.l.* during the Late Oligocene to Middle Miocene 12.6-27.6 Ma, supporting a recent and rapid diversification within most of these clades. The biogeographic origins of the lineages are reconstructed as Afrotropical (Physcomitrellopsis-Fifeobryum-Funariella clade & Entosthodon clade) and Palearctic (Amphoritheca clade) and the ancestral climatic niches are reconstructed as temperate steppe (Physcomitrellopsis-Fifeobryum-

Funariella clade), Mediterranean (Amphoritheca clade) and tropical (Entosthodon clade). The reduction of sporophyte morphology is an important evolutionary trend in the Funarioideae. Ancestral states of the seta, peristome and capsule shape were reconstructed in the Funarioideae. Character states were tested for correlated evolution and evolutionary rates of dual character-state change were compared. Exserted, zygomorphic, peristomate sporophytes were reconstructed as the ancestral type sporophyte. Evolution between i) the seta and the peristome and ii) the capsule shape and the peristome is correlated. Evolutionary rates of dual character-state change suggest an ordered sequence of morphological changes towards achieving a reduced sporophyte. This study significantly advances our understanding of evolutionary relationships in the Funarioideae, further providing evidence that the evolution of reduced sporophytes occurs through an ordered sequence of morphological changes. Long distance dispersal of spores and lability of the climatic niche are likely to have strongly contributed towards the contemporary distribution of *Entosthodon s.l.* and may in part explain the groups rapid diversification. This thesis contributes towards a growing understanding of bryophyte biogeography and the diversification of these early land plants.

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1. General Introduction

> "That evolution is a fact and that the astonishing diversity of animals and plants evolved gradually was accepted quite universally soon after 1859 [Darwin's: On the Origin of species]. But how this evolution proceeded, particularly the nature of its moving force, has been a source of controversy from the very beginning."
> -Ernst Mayr (1997, pg. 9)

The quest to understand the origins of life on earth and how it came to be so diverse is perhaps one of the single most significant goals of mankind and of science. The earliest evidence for life on Earth is the presence of biogenic graphites in 3.7 billion-year-old metasedimentary rocks in Western Greenland (Ohtomo et al., 2014), and microbial mat fossils found in 3.48 billion-year-old sandstones in Western Australia (Noffke et al., 2013). In almost 4 billion years, approximately one-third the estimated age of the universe, the number of eukaryotic species alone has flourished to an estimated 8.7 million (Mora et al., 2011), albeit with major dips associated with mass extinctions (Jin et al., 2000; Knoll et al., 1996; Roberts et al., 2001).

Carl Linneaus (Stearn, 1959) first proposed the modern system of nomenclature a mere 200 years ago, and since then we have documented almost 14 % of the diversity of life on earth (Mora et al., 2011). By documenting life we are

able to define the fundamental units of biodiversity and provide an objective base on which to organise and understand it. Documenting, however, is only the first step in understanding the diversity around us. What follows from that is the difficult part: piecing together the evolutionary story of its origins using evidence from DNA, morphology, physiology, behaviour and distribution. Significant advances in sequencing technology over recent years, coupled with novel analytical approaches made possible by rapid advances in computational ability, mean that biologists are now beginning to gain a more complete picture of life on earth and the processes that have resulted in the diversity we see around us.

However, as in all arenas of biology, the scope of such programmes depends crucially on a sound taxonomic base – how many species there are and what their morphological and geographical limits are. Whilst some groups, in some areas, can be considered nearly completely known, knowledge of many others is woefully incomplete. Filling these gaps is crucial to fully comprehending evolutionary processes and developing paradigms based on the full spectrum of life rather than a few, possibly atypical, model systems. In this thesis I attempt to fill such a gap for one moss genus - *Entosthodon* (Funariaceae) - in Africa.

1.1. Documenting diversity: the need for taxonomic studies

> "Taxonomy provides the bricks and systematics the plan with which the house of the biological sciences is built"
> R.M. May (2004, pg. 733)

Taxonomic studies, i.e. revisions and monographs, form a cornerstone of biological research and among their pages we find the clarification and explanation of the diversity of organisms that share our planet. Importantly, these studies provide definitive statements on a number of aspects including taxonomic

boundaries, nomenclatural history, classification of the group, keys for identification, information on distribution, ecological tolerances and conservation status (Stuessy and Lack, 2011). They represent our fundamental scientific knowledge base, underpinning our entire understanding of biodiversity.

Taxonomic studies play a fundamental role in providing hypotheses of relationships that are used to investigate aspects of the evolutionary process. Without the careful description of new species we would not know what the fundamental units of life are, how many of them exist, where they exist and what anatomical traits they share. The study of speciation and the origins of our planet's diversity would not be able to proceed if the relationships between taxa were not first established, i.e. there would be no hypotheses of relationships to study. Similarly for most fields of biological research, basic information on species is fundamental to conducting sound scientific research (Stuessy, 1993; Stuessy and Lack, 2011).

The need for taxonomy is surely at its greatest today. With growing global populations and the demands this is placing on natural habitats worldwide, we are facing a global biodiversity crisis. In the next century it is estimated that we could lose as much as two thirds of the world's biodiversity (Raven, 2004; Wilson, 1985), and an inestimable amount of evolutionary history with it. Fortunately, the number of practising taxonomists today is higher than it has ever been before (Costello et al., 2013) and recent advances in molecular sequencing in recent years have propelled taxonomic research to new heights allowing researchers to formally and objectively test systematic hypotheses and species identities.

1.2. Molecular phylogenetics: reconstructing the evolutionary, biogeographic and temporal framework

Since the time of Charles Darwin it has been the dream of many biologists to express the evolutionary histories among all living organisms on earth in the form

of a phylogenetic tree. To do this, early evolutionists used the methods of comparative morphology and comparative physiology (Nei and Kumar, 2000). This approach proved to be successful at recovering many of the major aspects of the evolutionary history of organisms but the complexity of evolutionary change in morphology and physiology prevented the production of a clear-cut picture of evolution (Nei and Kumar, 2000). This all changed with advances in molecular biology and the advent of methods for reconstructing phylogenetic trees from DNA data. For the first time, molecular data provided scientists with a fundamental feature that could be compared across all living organisms.

The impact of molecular data on the field of plant systematics has been profound. In combination with continually advancing methods for phylogenetic analysis, molecular data have reshaped concepts of relationships and circumscriptions at all levels of the taxonomic hierarchy (Crawford, 2000; Small et al., 2004). Nowadays, phylogenetic analyses almost always accompany taxonomic treatments, helping taxonomists determine species identities, test hypotheses of relationship between taxa and identify characters that can be used to circumscribe clades. Phylogeny has been used, for example, to discover the root of the angiosperms, thus providing a direction and temporal scale for angiosperm evolution (Savolainen and Chase, 2003). Studies of diversification rely on phylogenies to determine groups of interest i.e. those that may have radiated rapidly. However, molecular phylogenies are an integral component in many other areas of biological research, whether the question is orientated towards physiology, community or macroecology or biogeography, phylogenetic trees form the backbone of these studies and allow us to pose and answer questions in an evolutionary framework. The combination of phylogeny with other sources of data makes it an especially powerful tool that can be used, for example, to determine how limbs evolved in vertebrates and arthropods (Shubin et al., 1997) or infer what the an-

cestral habitats were in Poaceae (Bouchenak-Khelladi et al., 2010).

Spurred by an interest in comparative methods in evolutionary biology, ancestral character state reconstruction, also known as character optimization or character mapping (Omland, 1999), has seen much progress in recent years and has been embraced by systematists and evolutionary biologists. The method of reconstructing ancestral character states, however, is nothing new, as it relies on the same principles as those used to reconstruct the relationships among genes and infer phylogenies. The reconstruction of ancestral states has become a standard tool used to elucidate the processes shaping trait evolution along the branches of phylogenetic trees (Pagel, 1999b), and in principle making it possible to describe what the past was like. Traits such as physiology and behaviour, which do not fossilize, are possible to reconstruct thereby lending support to traditional palaeontological studies (Pagel et al., 2004; Pagel, 1999a). The applications of ancestral state reconstruction are many and the potential questions which can be asked are vast in number.

The field of biogeography in particular has benefited from the application of such methods and has undergone a revolution in recent years. Biogeographers are fundamentally concerned with understanding the distribution of taxa over the surface of the earth and through time. Biogeographers routinely use molecular phylogenies and reconstruction of ancestral states to determine, for example, how and why organisms have likely achieved their current distributions and what their likely origins were. The field has further benefited from the advent of molecular dating techniques that allow them to add a temporal component to their hypotheses and cross-validate this with reconstructions and fossil data.

Time-calibrated phylogenies are now an integral part of studies aimed at understanding key evolutionary processes as they allow the researcher to infer things like the geological context of lineage diversification (Newton et al., 2007;

Cowling et al., 2009; Göbbeler and Klussmann-Kolb, 2010; Shaw et al., 2010; Xie et al., 2014; Yoder and Yang, 2004; Jansa et al., 2006; Vargas, 2007), the role of long distance dispersal in shaping contemporary distribution patterns (Heinrichs et al., 2009; Bartish et al., 2011; Renner, 2004a; Lewis et al., 2014; Le Roux et al., 2014) or the origin of new ecological niches (Villarreal and Renner, 2014). The idea of dating evolutionary divergences using calibrated sequence differences was first proposed by Zuckerkandl and Pauling (1962, 1965). The authors postulated that the degree of difference between the DNA molecules of two species is a function of the time since their evolutionary separation. This was shown by comparing protein sequences from different species and further comparing amino acid substitution rates with ages estimated from fossils (Sauquet et al., 2012). The advent of relaxed-clock methods brought with it more flexible techniques of incorporating calibrations leading to a renewed interest into methods of calibrating estimates of divergence times (Graur and Martin, 2004; Yang and Rannala, 2006; Ho, 2007; Donoghue and Benton, 2007; Ho and Phillips, 2009). Because DNA sequences do not directly contain information on the period over which genetic variation has accumulated or the rate of substitution, a number of methods are employed to calibrate phylogenies. The use of a calibration point allows for the untangling of absolute time from total genetic divergence which is the product of the substitution rate and the time elapsed. Among the alternative methods employed to calibrate phylogenies, the use of fossil evidence is by far the most frequently used in dating studies (although for birds it is substitution rate: see Ho (2007)). There has been considerable debate on whether to use single or multiple calibration points, with most studies advocating the use of multiple calibrations to overcome potential error associated with single points of calibration (Yang and Rannala, 2006; Sauquet et al., 2012). Accompanying the use of fossils, however, is uncertainty in taxonomy and geology (age) and error

in either of these can have significant impacts on divergence estimates. It is not unheard of for studies to report divergence estimates that differ by more than double one estimate between different fossil calibrations (Sauquet et al., 2012), highlighting the difficulty of using fossil evidence. Heterochronous sequences of known age, such as ancient DNA sequences extracted from radiocarbon-dated samples have also been used as means to calibrate phylogenetic trees (Ho et al., 2008). Alternatively, workers have used biogeographic events such as the formation of oceanic islands (Warren, 2003; Heads, 2011) or the separation of continents (Upchurch, 2008) to estimate a maximum age of divergence. The accuracy of biogeographic calibrations depends on the availability of reliable geological dating, and are often based on assumptions about vicariance and dispersal and thus these calibrations need to be carefully considered (Ho and Phillips, 2009). In the absence of a good fossil record, as in the bryophytes, divergence times have been inferred using DNA substitution rates (Ho, 2007; Shaw et al., 2010; Villarreal and Renner, 2014; Lewis et al., 2014). Substitution rates, however, can vary dramatically across lineages and between different DNA markers and attention is required when applying such calibrations (Magallón, 2004; Weir and Schluter, 2008; Sanderson et al., 2004). Secondary calibrations, i.e. using a divergence estimate resulting from a previous dating study, are the least recommended form of calibration and are usually associated with a large degree of error (Shaul and Graur, 2002; Graur and Martin, 2004).

1.3. Plant biogeography: dispersal and vicariance

The study of biogeographic patterns has long interested and puzzled scientists. Of particular interest has been those taxa occupying disjunct distributions that are separated by vast distances e.g. across oceans or deserts. At first, early biogeographers believed these disjunctions to be the result of trans-oceanic disper-

sal events (Nelson, 1978), but with the reappraisal of plate tectonic theory in the 1970s the emphasis moved away from dispersal as an explanation, because it was inherently difficult to test or falsify, to vicariance, especially invoking continental drift as an explanation (Raven and Axelrod, 1974). Molecular data once again shifted the view back to the role of dispersal as these data started to reveal a lack of correlation between the ages of many lineages and the timing of continental break-ups (Xiang et al., 2000; Magallón and Sanderson, 2001; Wikström et al., 2001; Renner, 2004a; Queiroz, 2005).

Despite the increasing view that dispersal has played a much greater role than generally appreciated (Queiroz, 2005), the role of vicariance is still firmly established as a significant mechanism structuring the distributions of many taxa (e.g.angiosperms, Xiang et al. (2000); Crisp and Cook (2007)). This is not necessarily the case for spore producing plants, like mosses and ferns (Muñoz et al., 2004; Wolf et al., 2001). The greater dispersal ability of these plants means that they tend to occupy much larger ranges and it is not uncommon for species to have distributions that span multiple continents (Delgadillo, 1993; Muñoz et al., 2004; Wilding and Hedderson, 2011).

As a result, endemism tends to be much lower in comparison to the angiosperms because fewer barriers to successful dispersal exist. This is the case in even the most isolated volcanic archipelagos (Staples and Imada, 2006; Staples et al., 2004). Because distribution ranges are often much larger in bryophytes, endemism also occurs at much larger scales. For example, patterns of endemism observed in angiosperms at the family level are often observed at the level of genera and species in bryophytes (Goffinet and Shaw, 2009).

1.3.1. African plant biogeography

The African flora displays a high degree of patterning and its biogeographical regions have been well studied and documented (Linder, 2001; Linder et al., 1998, 2005, 2012; White, 1983). White (1983), in his seminal work, postulated 20 phytochoria in Africa and the adjacent islands, based primarily on zonal vegetation (comprising largely trees). More recently Linder et al. (1998) re-evaluated the phytochoria of sub-Saharan Africa using a more robust statistical procedure and found that in many instances the clusters obtained (Figure 1.1) were very similar to those of White (1983).

Six major areas of endemism are present in sub-Saharan Africa: the Cape Floristic Region, the East African coast, the Zambezi-Congo watershed, and the three rainforest centres of Kivu, lower Guinea and upper Guinea (Linder 2001). Richness is strongly related to maximum rainfall, but there are no obvious correlations between modern climate and endemism. Species richness and endemism north of the equator is much more concentrated into centres than south of the equator (Linder, 2001). Species richness in southern Africa is high (*ca*. 20 000), much richer than East Africa (*ca*. 11 000), while the flora of West Africa and the Zambezian basin are the poorest (*ca*. 7 000 species each, Linder, 2001). Little work has been undertaken on the distribution of African bryophytes. Recent checklists for Africa (O'Shea, 2006) and the neighbouring islands (Marline et al., 2012; Een, 2009; Ah-Peng and Bardat, 2005) and floras from southern (Magill and van Rooy, 1998; Magill, 1981, 1987), East (Chuah-Petiot, 2003) and West Africa Wigginton (2004) and parts of central Africa (Fischer, 2013) hold much distributional data for African bryophytes, but this information has yet to be distilled into a global picture of bryophyte biogeographic patterns on the continent and surrounding islands.

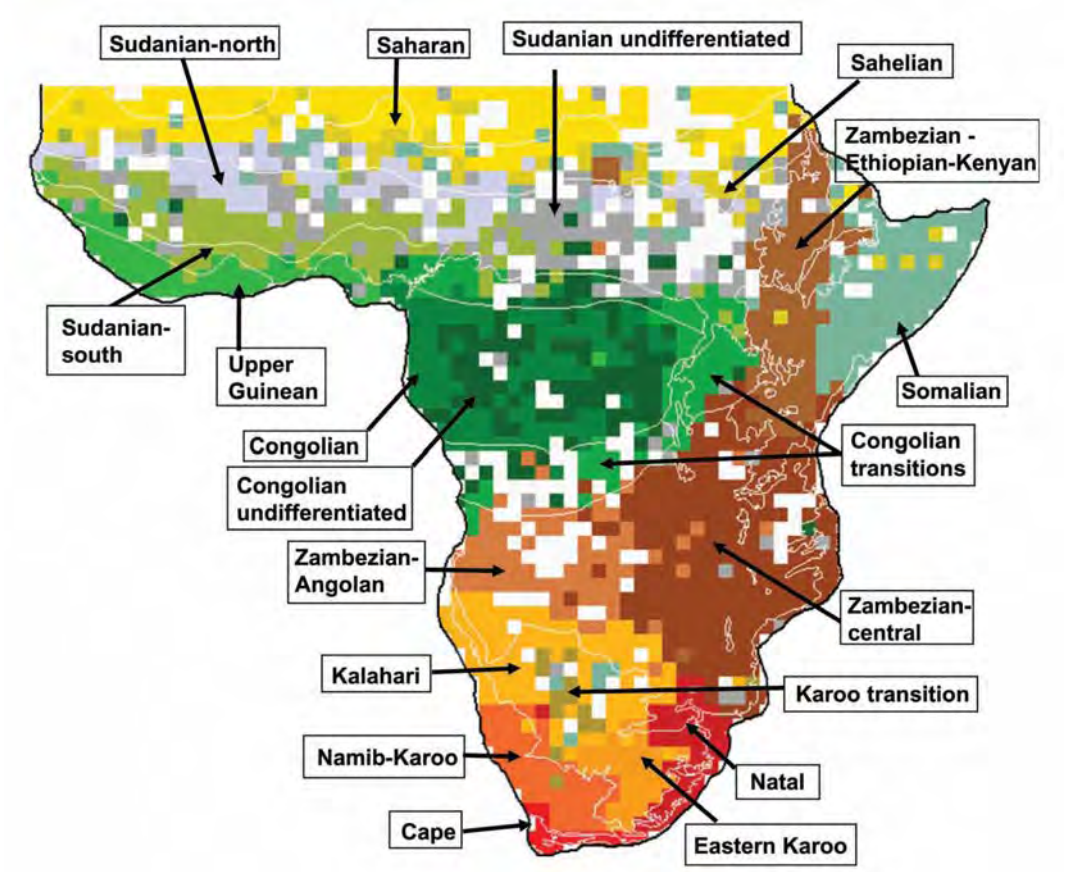

Figure 1.1: The plant phytochoria of sub-Saharan Africa. The boundaries of the White (1983) regions are indicated in white, and the phytochoria retrieved by Linder et al. (2005) colour coded. Figure taken from Linder et al. (2005).

On a smaller scale, Van Rooy and Van Wyk (2010), based on an analysis of the bryophyte flora of Southern Africa, described four major bryofloristic regions (Figure 1.2): i) a subtropical or palaeotropical region in the northern, eastern and southern parts, characterised by a predominantly mesophytic moss flora (subdivided into the Zambezian and Afromontane Regions); ii) a temperate or austral region in the central and western parts of the study area with a xerophytic moss flora (subdivided into the Karoo-Namib and Highlands Regions). These four bryofloristic regions are very similar to White's (1983) phytogeographic regions for vascular plants of southern Africa, although White (1983) recognizes

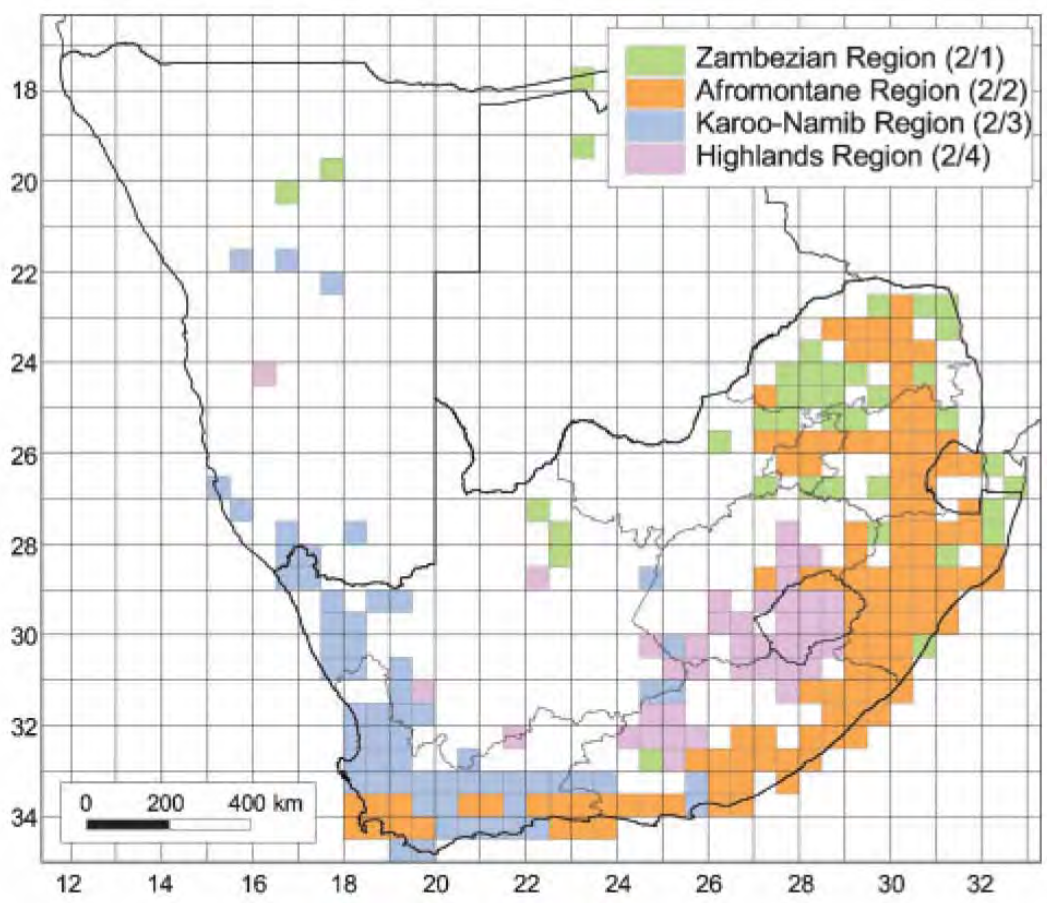

Figure 1.2: The four bryofloristic regions of southern Africa according to Van Rooy & Van Wyk (2010). Figure taken from Van Rooy & Van Wyk (2010).

an additional region, the Tongaland-Pondoland region which is absent in the Van Rooy and Van Wyk (2010) bryofloristic regions. The similarity of these biogeographic regions suggests that in part the patterns shaping the distribution of vascular plants probably act on spore dispersed plants like bryophytes too.

A major portion of the families (76 %) and genera (23 %) of southern African vascular pants are either cosmopolitan or pantropical. Approximately 25 % of genera (473) are endemic to the region. Very few genera show disjunct distributions with Eurasia (2.5 %), the New World (1.2 %) or are Gondwanan relics (1.2 %) (Goldblatt, 1978; Cowling et al., 2004). For comparison, the moss flora

of southern Africa has only 16 endemic genera (7 %) and one endemic family, the monotypic Wardiaceae (Zander and Hedderson, 2011; Van Rooy and Van Wyk, 2010; Hedderson and Zander, 2007a; Zander and Hedderson, 2009; Hedderson and Zander, 2008a,b). In global terms these figures are actually considered remarkably high for mosses. Wide ranging, disjunct distributions are, however, more common in bryophytes than vascular plants. For example, Delgadillo (1993) reports 334 moss taxa that are disjunct between Africa and the Neotropics and Gradstein (2013) reports 74 species of Afro-American liverworts.

1.4. The moss genus *Entosthodon* Schwägr. (Funariaceae)

1.4.1. The Funariaceae

The Funariaceae are a relatively large family (*ca*. 300 spp) of small, soil-inhabiting, annual to biennial mosses. Most species in the family display either an Annual-shuttle or Fugitive life-strategy, *sensu* During (1979), because the patches they inhabit are often ephemeral and/or prone to frequent disturbance e.g. steep, earthen-banks and edges of small streams. Many species in the family have wide, often disjunct, ranges, which can span two or more continents (Wilding and Hedderson, 2011). They occupy a variety of environments from tropical to temperate, alpine and Mediterranean climates, from sea level to mountain slopes exceeding 4000 m. Members of the family are well known for their ability to be cultivated easily in the lab and to form interspecific and intergeneric hybrids. (Fife, 1985). This feature has made them popular experimental organisms. Two species in particular, *Funaria hygrometrica* and *Physcomitrella patens*, are particularly well known for their role as model organisms (Bauer and Brosig, 1959; Bryan, 1957; v. Wettstein, 1924; Bassi et al., 2014; Sabovljević et al., 2014; Cove, 2005; Schaefer and Zrÿd, 2001) and *P. patens* was the first bryophyte to have its entire

genome sequenced (Rensing et al., 2008).

The sole character uniting members of the family and setting the Funariaceae apart from other mosses are the inflated to globose terminal cells of their paraphyses (Fife, 1985). A second character, although present in only the minority of species, sets the family apart from other mosses – the architecture of the peristome. The peristome is diplolepideous but the endostome teeth lie opposite the exostome teeth; the ontogeny of the inner peristome layer involves symmetric divisions that separate two consecutive segments (Liu et al., 2012; Goffinet et al., 1999; Schwartz, 1994; Shaw and Anderson, 1988).

Unlike most other mosses, the family is characterized by gametophytic uniformity and sporophytic plasticity (Fife, 1985). The dominant evolutionary trend in the family appears to be the gradual simplification of the sporophyte such that many traits related to dispersal are reduced or lost entirely (Fife, 1985). This direction may be the evolutionary consequence of selection for an increasingly ephemeral life history in line with the temporary to ephemeral habitats that they occupy. The frequency of these independent reductions across the family is remarkable and has resulted in the convergent evolution of similar sporophyte morphologies in different lineages (Fife, 1985; Liu et al., 2012; Beike et al., 2014; McDaniel et al., 2010). This has brought into question the validity of the current classification because characters of the sporophyte have traditionally been used to circumscribe supra-specific taxa in the family.

The family comprises 16 genera, the largest of which are *Funaria, Entosthodon* and *Physcomitrium* each with *ca*. 90 species (Tropicos, 2003; Ignatov et al., 2015). The three genera together make up *ca*. 95 % of the diversity in the family, holding all but 17 species. Of the remaining genera, 11 are monotypic and two comprise three species (*Physcomitrella* and *Goniomitrium*) (Liu et al., 2012). Many of the monospecific genera have been traditionally grouped together be-

cause they share similar reduced morphologies. Recent phylogenetic work, however, suggests that relationships between these genera and their placement within the Funariaceae (see Figure 1.3) may be more complex than originally expected (Beike et al., 2014; Liu et al., 2012; McDaniel et al., 2010).

Within the Funariaceae, the Funarioideae comprises 14 genera and 99 % of the diversity (*ca*. 280 spp.) while the genetically divergent Pyramiduloideae comprises only the genera *Pyramidula* and *Goniomitrium* and 1 % of the diversity (4 spp.)(Liu et al., 2012). The phylogenetic relationship between the sub-families is shown in Figure 1.3. I thus consider the Funarioideae to comprise the ”core” Funariaceae and do not consider the genetically divergent Pyramiduloideae from here on.

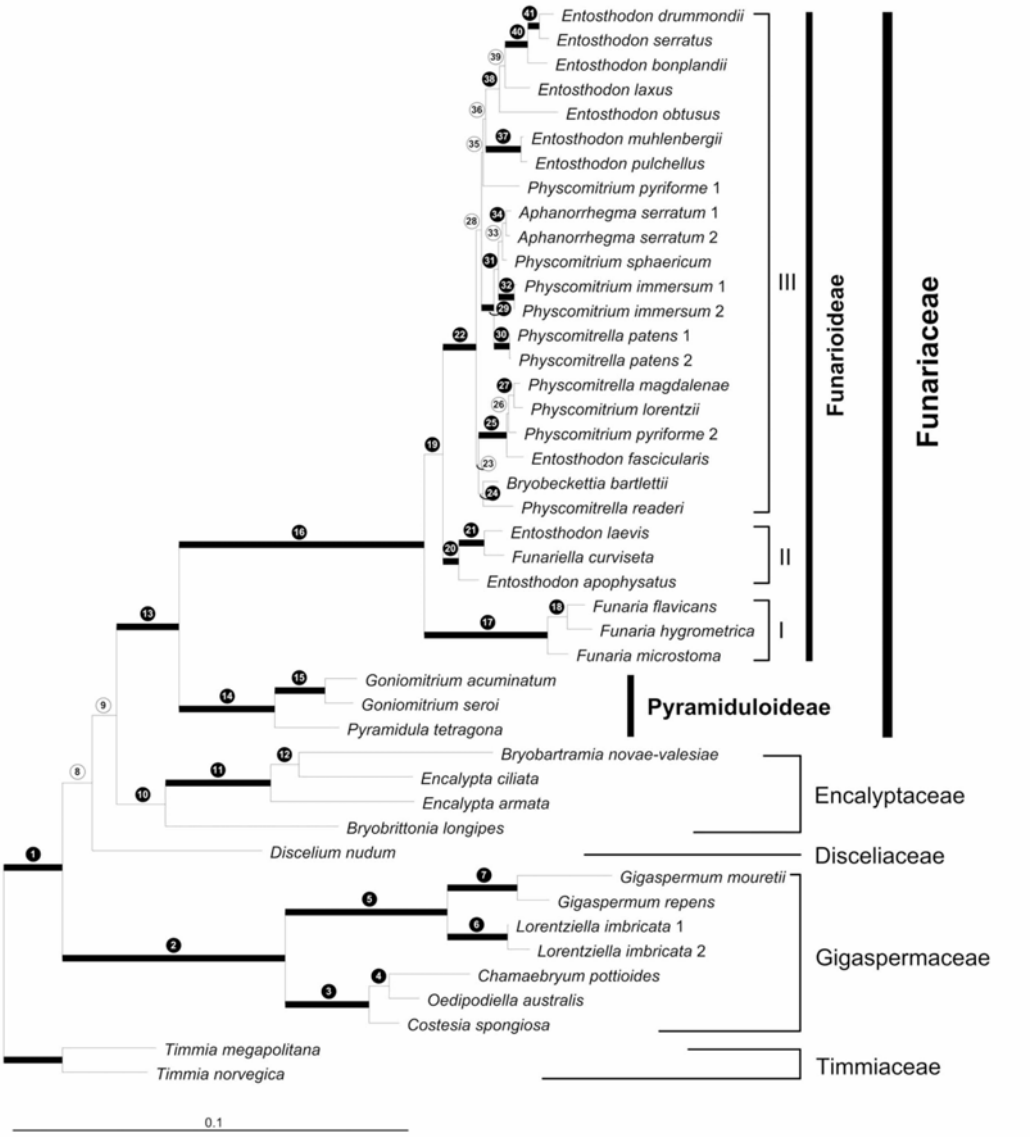

Figure 1.3: Maximum-likelihood phylogram of the Funariaceae, based on a 10-gene dataset. Figure taken from Liu et al. (2012). Thickened branches received 100 % MP, ML bootstrap and 1.00 BI posterior probability support. Filled circles indicate nodes receiving strong support (MP and ML > 90 % and BI > 0.95). Empty circles indicate nodes with only moderate (70 % < MP and ML < 90 % and/or 0.90 < BI < 0.95) to weak (MP and ML < 70 % and/or BI < 90 %) support in one or multiple analyses. Group names are listed on the right side of the tree.

The circumscription of two genera within the Funarioideae, *Entosthodon* and *Funaria*, has long troubled taxonomists with *Entosthodon* often being recognized as a sub-genus of *Funaria* (Lindberg 1870; Brotherus 1903). Fife (1985), however, in his generic revision of the Funariaceae concluded that *Entosthodon* should be distinguished from *Funaria* based on the absence of a compound, revoluble annulus in the former. This use of the annulus to distinguish the two genera is supported by recent phylogenetic work on the family (Liu et al., 2012).

1.4.2. *Entosthodon*

The genus *Entosthodon* Schwägr., is estimated at *ca*. 90 species worldwide (Tropicos, 2003). The genus has been revised for the South American Andes where 10 species were recognised (Fife, 1987), and more recently the seven species occurring in Australia (Fife and Seppelt, 2001). The European and North American species are few in number and relatively well-known, appearing in numerous floras (Smith, 2004; Crum and Anderson, 1981; Brugués et al., 2010), whilst the flora of Macaronesia and the Mediterranean has received attention from Dirkse and Sergio (2001); Brugues (2000); Dirkse and Brugués (2010); Brugués et al. (2010, 2001); Brugués (1998); Brugués et al. (1999). The Asian species were treated by Eddy (1996) who recognised four species in his flora of Malesian mosses and the flora of the Caucasus has been worked on by Fedosov et al. (2010). The African species have never been subject to revision but species have been treated in two local floras (see section 1.4.3 below).

At present, circumscription of the genus is based on combinations of characters states with no single character or state defining the genus. Similar problems are encountered at a subgeneric level; quoting Fife (1982): “the delimitation of *Entosthodon* and its intrageneric taxa is the most difficult taxonomic problem in the Funariaceae”. Recent molecular studies are now suggesting that *Phys-*

comitrium, a closely related genus, may present similar difficulties (Beike et al., 2014; McDaniel et al., 2010; Liu et al., 2012).

Taxonomic problems are undoubtedly largely a result of the evolutionary simplification of the sporophyte and the fact that sporophytic characters are plagued by homoplasy as shown by Liu et al. (2012). Liu et al. (2012) provided the first evidence that (i) *Entosthodon* is paraphyletic (see Figure 1.3 above), casting significant doubt on the current circumscription of the genus, and (ii) that homoplasy of important taxonomic characters is rampant across the family, subsequently bringing into question the taxonomic value of sporophytic characters for the circumscription of supraspecific taxa.

1.4.3. *Entosthodon* in Africa

Regional floras, with the exception of Magill's (1998; 1981; 1987) and Sim's (1926) floras of Southern Africa, are mostly lacking for African mosses. As a result the majority of the African species of *Entosthodon* have received little mention or treatment in the literature since their first description. A number of checklists have been published for parts of Africa, the most recent and comprehensive being O'Shea's (2006) checklist of the mosses of sub-Saharan Africa which lists 36 species of *Entosthodon sensu* Fife (1985). Of these, 27 are species described from African material while the remaining 9 are records of wider ranging, often European, taxa. All 27 African species are endemic to the region. The diversity of *Entosthodon spp*. per country, according to (O'Shea, 2006), is mapped below (Figure 1.4).

Among the most prominent authors of African names are J.K.A. Müller, W. Mitten, H.N. Dixon and E. Bescherelle, who between them are responsible for half of the published names (O'Shea, 2006). Species of *Entosthodon* are unknown for many countries in sub-Saharan Africa. This, I believe, reflects a general lack of

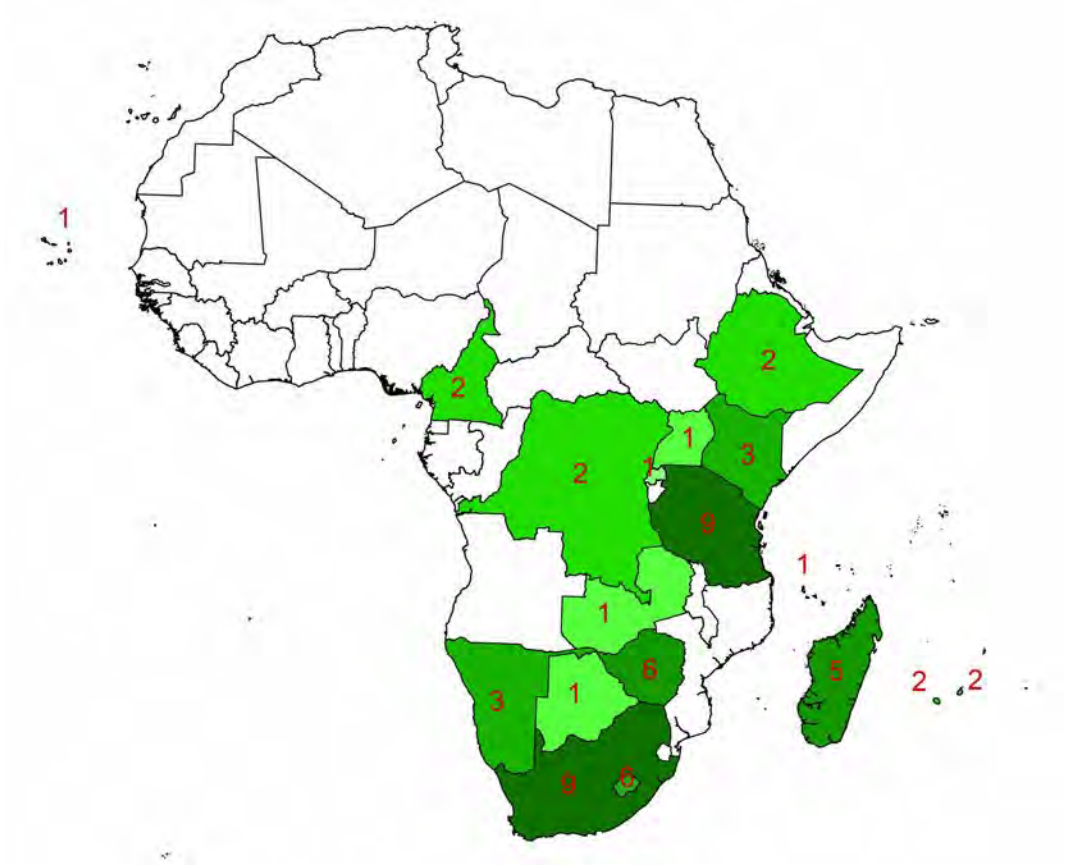

Figure 1.4: Species diversity of *Entosthodon* in sub-Saharan Africa, by country, according to O'Shea (2006).

bryological exploration in these areas rather than the absence of the genus. For example, out of the 65 sub-Saharan African countries included in his checklist of mosses, O'Shea (2006) records 36 countries that have fewer than 100 species recorded and 9 countries that have fewer than 10 species recorded. Two centres of diversity are evident at this stage, one in South Africa and one in Tanzania. This corresponds well to at least two of the major areas of plant endemism discussed in section 1.3.1 above, but probably also reflects to some degree the amount of bryological exploration these areas have received.

In this thesis, I plan to explore the evolutionary history of the genus *Entosthodon*. I use a phylogenetic approach to reconstruct relationships within the

genus and among the major lineages of the Funariaceae (Chapter 2) and use this setting to gain a glimpse into their diversification in time and space (Chapter 3). In addition, I examine more closely the evolution of reduced sporophyte morphologies in the family (Chapter 4). Lastly, I provide a taxonomic revision of *Entosthodon* in sub-Saharan Africa (Chapter 5). More specifically, some of the questions I wish to answer in this thesis are: What are the phylogenetic relationships among species of *Entosthodon* and between other members of the family? Do morphological characters exist that can be used to circumscribe molecular clades? (Chapter 2); When did *Entosthodon* start to diversify and did the group recently undergo a rapid radiation? What is the biogeographic history of the genus and is it comparable to that of other bryophytes? (Chapter 3); What are the ancestral sporophytic characters states in *Entosthodon*? Is the evolution of these characters correlated and, if so, does evolution of reduced morphologies occur through the random loss of complex states or by an ordered sequence of character state changes? (Chapter 4).

2. The Evolutionary Context: a phylogenetic hypothesis for *Entosthodon*

2.1. Introduction

The moss genus *Entosthodon* (Funariaceae) is present on every continent with the exception of Antarctica and is a well recognized component of many terricolous systems from sea level to elevations over 4000 m. It has received only cursory attention (Liu et al., 2012) outside of the taxonomic literature, most likely because the species for many parts of the world remain poorly known and are often approached with much apprehension.

In general, the Funariaceae are characterized by a relatively uniform vegetative body plan in comparison to the broad range seen in architectural complexity of the sporophyte (Fife, 1985). A dearth of useful morphological characters has been a major impediment for taxonomic work on the family. Accordingly, the majority of genera in the Funariaceae have been defined by a combination of sporophytic character states of which individual states often occur in more than one genus. This has lead to major taxonomic problems in the family, especially in the segregation of *Funaria* from *Entosthodon* as both genera include taxa with well developed peristomes and inclined capsules as well as many with upright capsules and variously reduced peristomes. To resolve this, many authors (Brotherus, 1903, 1924; Brotherus et al., 1925; Crum and Anderson, 1981;

Lindberg, 1879, 1870; Smith, 1978) adopted a broad concept of *Funaria* which included all species with the previously mentioned character states. Fife (1985), however, in his generic revision of the family, concluded that *Funaria* should be distinguished from *Entosthodon* based on its compound annulus: rings of cells which aid the shedding of the operculum from the sporangium. Apart from the annulus in *Funaria*, there are few character states that are restricted to individual genera of Funariaceae, with the current circumscription of *Entosthodon* completely unsupported by any obvious synapomorphies.

In his generic revision of the Funariaceae Fife (1985) recognized three subgenera of *Entosthodon* defined largely by the orientation of the capsule or the shape of the exothecial cells. Members of *E. subg. Plagiodus* possess inclined, zygomorphic capsules while those of *E. subg. Entosthodon* and *E. subg. Murcia* have upright and more or less radially symmetric capsules. The sole member of *E. subg. Murcia, E. fascicularis,* is further differentiated by its isodiametric to elongate exothecial cells, as opposed to purely elongate, which are more akin to members of *Physcomitrium* (Fife, 1985). Recent work shows that the current circumscription of *Entosthodon* is not congruent with phylogeny. Recent efforts by Liu et al. (2012) to resolve generic relationships in the family based on 10 loci from three genomic compartments, failed to fully resolve relationships amongst the major Funariaceae lineages. This study did, however, provide evidence supporting Fife's (1985) circumscription of *Funaria* and the first evidence to suggest that *Entosthodon* may be paraphyletic, comprising no fewer than three separate lineages. These authors also demonstrate that a sporophyte-based classification of the Funariaceae is particularly problematic because of rampant homoplasy in the architecture of the sporophyte, and concluded that these traits are either symplesiomorphies or homoplasious (McDaniel et al., 2010). Liu et al. (2012) attributed the lack of phylogenetic resolution to a recent and rapid radiation of the

family. As shown below (Chapter 5), 26 species of *Entosthodon s.l.* are known from sub-Saharan Africa. These occur mostly in southern and East Africa, and combined these areas harbour > 70 % of the total known species-level diversity in sub-Saharan Africa. The African species have not formed part of any phylogenetic study and relationships among the species remain unknown.

The aim of this chapter is to i) evaluate the phylogenetic relationships of species assigned to *Entosthodon*, both to each other and to other members of the Funariaceae or more specifically the Funarioideae; ii) to determine whether morphological characters exist that can be used to circumscribe major molecular clades; and iii) determine whether African species of *Entosthodon* form a monophyletic group, or comprise several phylogenetically independent lineages.

2.2. Materials and Methods

2.2.1. Taxon and gene sampling

To reconstruct phylogenetic relationships of *Entosthodon*, 140 exemplars (see Appendix A, Table A.1) representing nine genera, 67 species and one variety with a total of 45 species of *Entosthodon* (representing at least 50 % of the global diversity) were included and rooted with *Funaria* as the outgroup. The sampling attempts to represent, as far as possible, the major lineages of the Funarioideae, at least as these are currently understood. To avoid a sampling bias, this study attempted to sample as many species of *Entosthodon* as possible from around the world. Eighteen African species are sampled here; those species remaining unsampled are known only from type collections or from collections that are too old to sequence. A paucity of recent collections of *Entosthodon* from south and south-east Asia limited sampling of species from this area; although the flora of

the region is not thought to be particularly diverse (Dandotiya et al., 2011; He and Gao, 2003; O'Shea, 2003).

Four chloroplast (cp) DNA loci were targeted: the noncoding spacer between the *atp*B and *rbc*L genes (*atp*B–*rbc*L), *psb*A–*trn*H noncoding region (*psb*A–*trn*H), ribosomal small protein 4 gene (*rps*4) and *trn*L (UAA)-*trn*F (GAA) region (*trn*L–F). Primer sequences were those used by (Liu et al., 2012). These loci were the most informative of the 10 used by Liu et al. (2012) to reconstruct generic relationships within the Funariaceae, and have been widely used in other bryophyte phylogenetic studies (Stech and Quandt, 2010). The nuclear ITS locus, often used for species-level phylogeny reconstruction, was not available because of the presence of multiple copies of variable lengths (Y. Liu personal communication - June 2012). The addition of non-maternally inherited markers in addition to chloroplast genes would have been ideal, however, given difficulties in amplification of nuclear genes this was not feasible given the time frame of the thesis. Liu et al. (2012) used 4 mt-DNA loci in their 10 gene phylogeny, however, these loci were not particularly variable and contributed relatively little phylogenetic information.

2.2.2. DNA extraction, amplification and sequencing

Total DNAs were extracted from air-dried herbarium specimens using a modified CTAB approach (Doyle, 1987). Polymerase chain reactions were prepared in 30 ul total volumes using KAPA Taq ReadyMix with dye (Kapa Biosystems) following the manufacturer's specifications. Amplification followed the same profile in each case: 95°C for 1 min followed by 30 cycles of denaturation (1 min at 95°C), annealing (1 min), extension (1 min at 72°C), and a final extension at 72°C for 7 min. Amplicons were purified using Fermentas Exonuclease 1 and FASTAP

following the manufacturer's specifications. All amplicons were sequenced using the PCR primers and these reactions were performed using the ABI PRISM BigDyeTM ver. 3.0 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) optimized for half- or quarter-size reactions. Sequencing products were purified using Sephadex G-50 (Amersham, Piscataway, NJ, USA) gel filters, and then separated by capillary electrophoresis using an ABI PrismTM 3100 Genetic Analyser.

2.2.3. Alignment and phylogenetic analyses

Sequences were initially aligned with MUSCLE 3.8.31 (Edgar, 2004) and later corrected by eye. Ambiguously aligned regions were eliminated from the final matrix using Gblocks 0.91b (Castresana, 2000) on the least stringent settings. Indel characters were coded using SeqState 1.4.1 (Müller, 2005) using the simple coding approach. Each coded indel was double-checked against the sequence alignment in order to rule out any miscoding, and indel characters originating within homopolymer regions were not coded to avoid unwarranted assumptions on homology.

Partitioning of the data set may have a strong effect on the topology and estimates of nodal support (e.g. Brown and Lemmon, 2007; Li et al., 2008; McGuire et al., 2007). To test for the optimal partitioning scheme and models of molecular evolution the open source software PartitionFinder v1.1.1 was used (Lanfear et al., 2012). Optimal schemes and models were chosen based on the Bayesian Information Criterion (BIC). BIC was chosen over the more widely used Akaike information criterion (AIC) for two reasons. First of all, the AIC (unlike the BIC) makes the somewhat unrealistic assumption that candidate models are all close to the true model (Sullivan and Joyce, 2005). Second, the AIC has been claimed to introduce redundant model parameters (Abdo et al., 2005). The DNA data

were analysed as a single partition, with a GTR+I model of nucleotide substitution, in accordance with the best partitioning scheme suggested by PartitionFinder. Phylogenetic relationships were inferred using Bayesian (BI) and Maximum Likelihood (ML) methods. The Bayesian posterior probability (B-PP) and ML bootstrap (ML-BS) are two alternative methods for assigning confidence to phylogenetic results. Although no consensus exists as to which method is more 'reliable', the B-PP has garnered much recent support because of its clear interpretation, computational efficiency and increased sensitivity to phylogenetic signal (Erixon et al., 2003). Much support still exists for the ML-BS because it is a more conservative measure of confidence and is less prone to type-I error (Erixon et al., 2003) on short internodes. Simulations have shown, however, that under the correct model B-PPs are still more efficient at assigning high confidence to true clades than the ML-BS (Alfaro 2003). When used in conjunction, they may both be of value for the assessment of phylogenetic results because each measures a different quality of the data.

Bayesian analysis was conducted using MrBayes version 3.2.1 (Ronquist and Huelsenbeck, 2003). The analysis was performed with two runs of four chains, with trees and parameters sampled every 1000th generation for 5 million generations. The indel matrix was analysed in a separate partition using the restriction model for binary data. Graphical exploration of the output from phylogenetic MCMC simulations gives intuitive and often crucial information on the success and reliability of the analysis (Wilgenbusch et al., 2004). MCMC performance was carefully assessed for convergence, mixing, and sampling intensity. The standard deviation of split frequencies was monitored for values below 0.01, which are a good indication of convergence (Ronquist et al., 2005). The Potential Scale Reduction Factor (PSRF) was monitored for all model parameters. A PSRF value close to 1 indicates good sampling from the posterior probability

(Ronquist et al., 2005). Five plots of the MCMC output from MrBayes were examined in AWTY (Wilgenbusch et al., 2004): 1) trace plots of log-likelihood values were assessed for stationarity, for separate runs; 2) convergence was assessed by checking for strong correlations in bivariate plots of split frequencies for the two runs; 3) cumulative split frequencies for a number of splits, for each run, was assessed for lack of a trend - trends diagnose a lack of convergence; 4) cumulative split frequencies and the corresponding presence or absence of a single split, between runs, was checked for a lack of a trend - trends diagnose a lack of convergence; 5) symmetric tree difference score within and between runs was checked - a between-run distance well separated from the within-run distance diagnoses a lack of convergence (Wilgenbusch et al., 2004). Methods used to assess convergence were according to those found in Wilgenbusch et al. (2004) and in the MrBayes 3.1 Manual (Ronquist et al., 2005). Trees were summarized after removing the burn-in samples and a 50 % majority-rule consensus tree was built in MrBayes.

Maximum likelihood analysis was performed using Garli 2.0 (Zwickl, 2006). The program was run twice, with five replicates each time, using the default settings and the automated stopping criterion. The tree with the highest likelihood score was chosen as the best tree. Statistical support for branches was assessed by non-parametric bootstrapping with 100 pseudoreplicates. The indel matrix was again analysed in a separate partition using the Mk model for binary data. To obtain a majority rule consensus tree, bootstrap proportions were summarized using the program SumTrees, DendroPy package (Sukumaran and Holder, 2010).

2.3. Results

2.3.1. DNA Sequencing and Alignment

Of a potential 560 sequences, 22 are missing of which 13 are *rps*4 accessions and three accessions are missing from each of the remaining three loci. Information on accessions is shown in Table A.1 of Appendix A. Alignment of the four plastid loci yielded a combined data matrix of 2288 bp which, following the exclusion of ambiguous regions, was reduced to 1994 bp prior to the analyses. Sequence data characteristics are summarized in Table 2.1. The *trn*L-F region was the most variable of the four loci used and also provided the most indel characters. A total of 100 indels was identified for the four loci; however, after careful inspection of the coded matrix, only 70 were regarded as being unambiguously codeable.

Table 2.1: Characteristics of the four loci used in the phylogenetic reconstruction.

	atp B-*rbc* L	*psb* A-*trn* H	*rps* 4	*trn* L-F
Length	710	448	580	550
No. of complete sites (no gaps, no N)	261	367	478	283
No. of variable sites	64	55	71	137
No. of indels scored	24	9	8	29

2.3.2. Phylogenetic resolution

The results from the BI and ML analyses did not differ considerably. Bayesian analyses usually provided higher support and better resolution than ML analyses. Relationships among the core clades remain a problem within the Funarioideae. The additional sampling did not completely resolve the poorly supported nodes recovered in the Liu et al. (2012) phylogeny. Of particular concern are the phylogenetic position of Entosthodon II and the monophyly of Entosthodon III, see

2.1. Alternative topologies could involve: i) Entosthodon II and III forming a clade, ii) Entosthodon II sister to Physcomitrium, or iii) cleavage of Entosthodon III. Alternate reconstructions usually comprised Entosthodon II and III sister.

2.3.3. Phylogenetic reconstruction

Posterior probabilities were not sensitive to the branch length prior for the BI analysis, and total tree length in the 50 % majority rule tree deviated by only 0.3 units between 3 independent MrBayes runs. The ML analysis produced a similar overall topology to the BI analysis. The Bayesian phylogeny is shown in Figure 2.1; thick, black branches have high Bayesian posterior probabilities (≥ 0.95) and high bootstrap support ($\geq$ 90 %), whilst thick, gray branches are strongly supported (≥ 0.95) in the Bayesian analysis only.

Entosthodon, as currently circumscribed, is non-monophyletic, and resolved within four major lineages across the tree: Entosthodon I, II, III and Physcomitrium. Lineages were designated based on phylogenetic divergence and named by the genus comprising the majority of the diversity in that lineage. The first split in the tree separates the outgroup, a lineage (PP=1, BS=100) comprising species of *Funaria* (*sensu* Fife (1985)), from a clade (PP=1, BS=100) comprising the four above-mentioned lineages. Entosthodon I (PP=0.99, BS=53) is sister to a strongly supported clade (PP=1, BS=99) comprising Entosthodon II, III and Physcomitrium. Within this clade, Entosthodon II (PP=0.97, BS=69) is sister to a clade (PP=0.84) present only in the BI analysis comprising Physcomitrium (PP=1, BS=78) sister to Entosthodon III (PP=1, BS=100). This is the only major difference between ML and BI analyses.

Only a single species of *Entosthodon, E. hungaricus* (Boros) Loeske, is resolved in the Physcomitrium clade, which otherwise contains only members of

Physcomitrium, Physcomitrella and other allied genera. *E. hungaricus* forms a clade (PP=1, BS=100) with two accessions of *Physcomitrium pyriforme* (Hedw.) Hampe from North America, sister to the rest of the Physcomitrium lineage.

Entosthodon I comprises 10 *Entosthodon* species, 3 *Funaria* (*Entosthodon sensu* Fife (1985)), and the monotypic genera *Physcomitrellopsis* and *Funariella*. Two well-supported clades are resolved within this lineage. The first (PP=0.86, BS=91) consists of the South African *Physcomitrellopsis africana* Wager & Broth. *ex* Dixon sister to the Dixonii clade. Within the Dixonii clade, the southern African

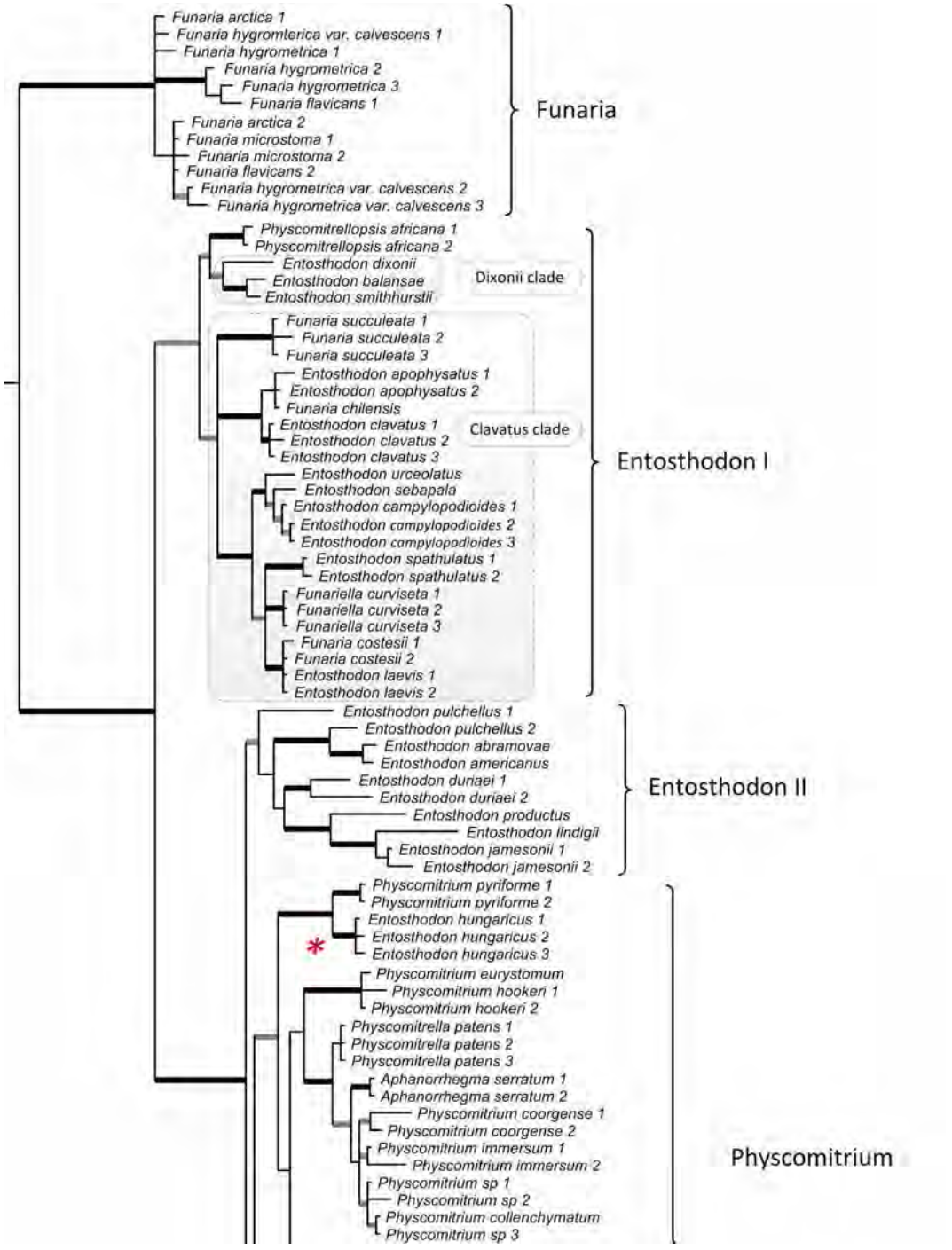

Figure 2.1: Bayesian 50 % majority rule consensus tree from the analysis of four cpDNA loci and coded indel data. Thickened black branches received high Bayesian posterior probabilities (≥ 0.95) and high bootstrap support (≥ 90 %). Thick gray branches received strong support (≥ 0.95) in the Bayesian analysis only. Names of clades were assigned based on the genus comprising the highest diversity. The star denotes the position of a single species of *Entosthodon* which is resolved in the Physcomitrium clade. Figure continued on next page

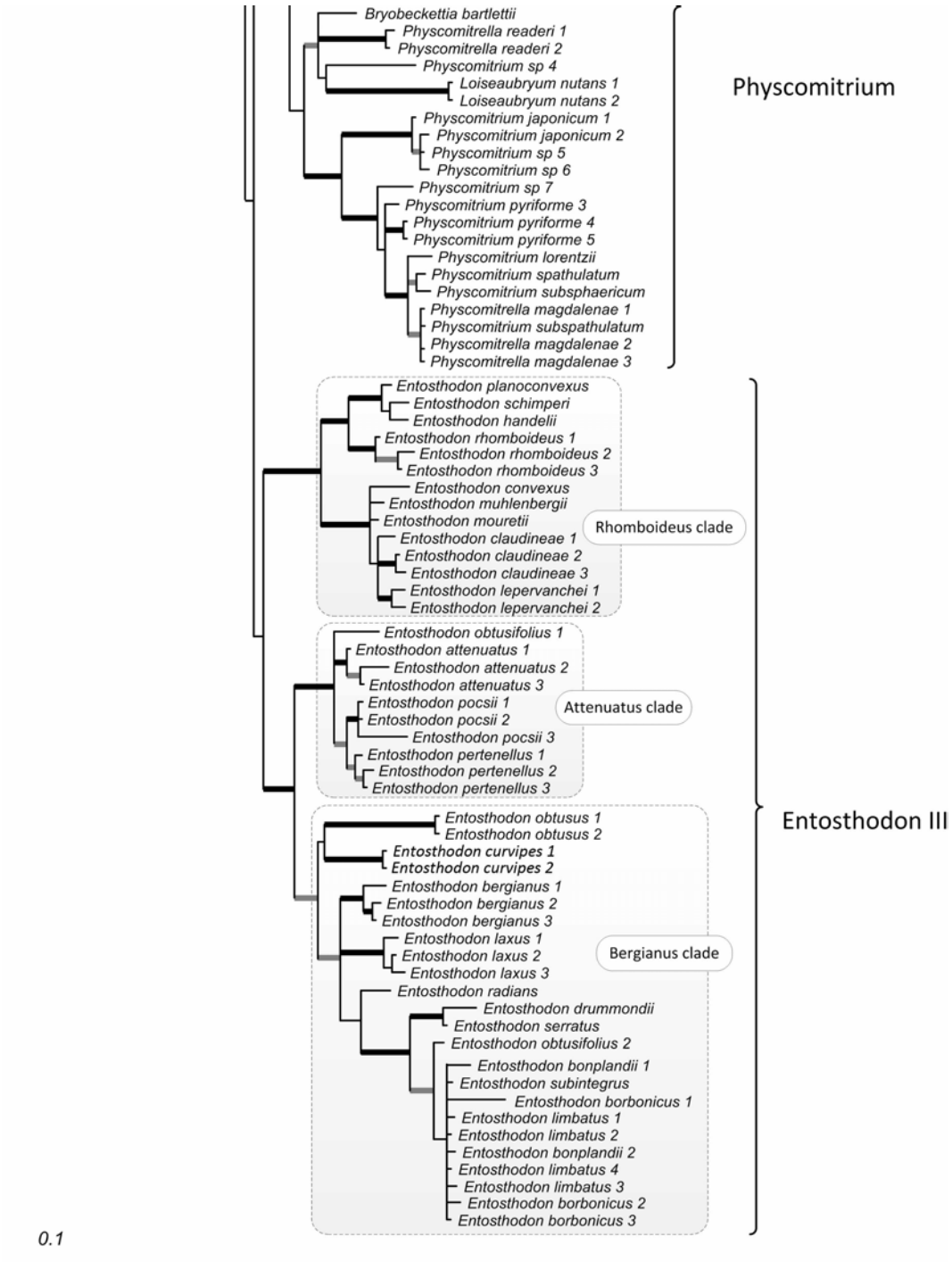

Figure 2.1. (continued).

E. dixonii Sim is sister to a clade comprising the South American *E. balansae* Besch. and Australian *E. smithhurstii* (Broth. & Geh.) Paris. The second clade (designated the clavatus clade; PP=0.98, BS=54) comprises 12 species in which two main clades form a polytomy with *F. succuleata* (Wager & C.H. Wright) Broth. ex Magill. In the first clade (PP=1, BS=100), the South African *E. clavatus* Mitt., is sister to a group comprising the Australian/South American disjunct, *E. apophysatus* (Taylor) Mitt., and the Chilean *Funaria chilensis* (Thér.) Thér.. In the second clade (PP=1, BS=98), *Entosthodon urceolatus* Mitt. from South Africa is sister to *F. sebapala sp. nov.* (see Chapter 5 for description) from Lesotho and the South African *E. campylopodioides* Müll. Hal. and these together are sister to a group (PP=1, BS=88) consisting of the South African species, *Entosthodon spathulatus* (Schimp. ex Müll. Hal.) Sim, in a polytomy with the Mediterranean-Macaronesian *Funariella curviseta* (Schwägr.) Sérgio and a clade comprising two South American species, *Funaria costesii* Thér. and *Entosthodon laevis* (Mitt.) Fife.

Entosthodon II includes seven species currently recognized under *Entosthodon*. The first split separates an accession of *E. pulchellus* (H. Philib.) Brugués from the Mediterranean from a clade comprising: the North American *E. americanus* (Lindb.) Fife and the Russian *E. abramovae* Fedosov & Ignatova sister to a second accession of *E. pulchellus* and sister to this is a clade containing two accessions of the Mediterranean-central Asian *E. duriaei*, sister to a clade comprising the Australian *E. productus* Mitt., sister to the Neotropical-African disjunct *E. lindigii* (Hampe) Mitt. and the pantropical species *E. jamesonii* (Mitt.)

Entosthodon III comprises twenty-six species of *Entosthodon sensu* Fife (1985). For ease of discussion it is split into three clades, with a perfectly-supported (PP=1, BS=100) Rhomboideus clade sister to a maximally-supported (PP=1, BS=100) Attenuatus + Bergianus clade. The initial split in the Rhomboideus

clade is also between two maximally supported groups. In the first of these *E. rhomboideus* Shaw from southern Africa is sister to a clade comprising *Entosthodon planoconvexus* (E.B. Bartram) Grout from North America sister to the central Eurasian *E. handelii* (Schiffner) Lazarenko + the Mediterranean *E. schimperi* Brugués. The second clade comprises *E. convexus* (Spruce) Brugués and *E. mouretii* (Corb.) Jelenc from the Mediterranean in a polytomy with the widespread temperate species *E. muhlenbergii* (Turner) Fife and a poorly-supported clade comprising two African species, *E. lepervanchei* Besch. and *E. claudineae sp. nov* (see Chapter 5 for description).

The Attenuatus clade comprises a well-supported (PP=1, BS=100) clade of two African species, *E. pertenellus* (Broth.) Kis and *E. pocsii sp. nov.* (see Chapter 5 for description) in a polytomy with the type of the genus, the European-American *E. attenuatus* (Dicks.) Bryhn and the Central-South American *E. obtusifolius* Hook. f..

The Bergianus clade comprises 12 species in a well supported clade (PP=1, BS=84). Apart from monophyly of accessions at the species-level, relationships within this group are poorly resolved. The East African *E. curvipes* Müll. Hal. and *E. obtusus* (Hedw.) Lindb. form a poorly-supported group sister to a clade, comprising the remainder of the taxa, that is well supported under Bayesian Inference. The South African *E. bergianus* (Hornsch.) Müll. Hal. and the circumsubantarctic-Andean *E. laxus* (Hook. f. & Wilson) Mitt. form a trichotomy with a clade comprising another South American-Australasian species, *E. radians* (Hedw.) C. Müll, poorly supported as sister to a group comprising a well-supported *E. drummondii* Sull and *E. serratus* (Brid.) Fife grouping from North America, sister to a clade containing a second disparate accession of *E. obtusifolius* sister to a final crown clade. The crown clade comprises a polytomy of the following species: *E. bonplandii* (Hook.) Mitt. from the neotropics, the Hawaiian endemic *E. subintegrus*

(Broth.) H.A. Mill., H. Whittier & B. Whittier, *E. limbatus* Müll. Hal. from southern Africa, and *E. borbonicus* Besch. from sub-tropical to tropical Africa.

2.4. Discussion

The four cp-DNA markers used in this study provide an overall well-supported phylogeny for the subfamily and the results presented here correspond well with previous work on the group (Liu et al., 2012; McDaniel et al., 2010). This is the most comprehensive phylogenetic reconstruction for the Funarioideae to date and the first to focus on the systematic relationships of the diverse and biogeographically significant genus *Entosthodon*. The analyses presented here provide fairly conclusive evidence that *Entosthodon* as currently circumscribed is paraphyletic as it has embedded within it genera such as *Physcomitrellopsis, Funariella* and the *Physcomitrium – Physcomitrellopsis* complex. Additionally, the analyses provide evidence for the existence of four main lineages within this larger group.

Weak support for some branches leaves some uncertainty in the relationships both within and between some of the major clades i.e. Entosthodon II, III and Physcomitrium. The current circumscription of the subgenera in *Entosthodon* is not congruent with the phylogenetic relationships presented here. Species traditionally comprising *E. subg. Plagiodus* are scattered across the tree and are present in each of the three major *Entosthodon* lineages. Whilst the same is true of *E. subg. Entosthodon* the majority of species fitting this subgenus occur within the Bergianus clade of *Entosthodon* III. The single species of *E. subg. Murcia, E. fascicularis* (Hedwig) C. Müller, is not represented in the phylogeny but based on its morphology it is likely to prove closely related to *E. hungaricus* which is resolved within the Physcomitrium lineage. The paraphyly of *Entosthodon* was

previously demonstrated by Liu et al. (2012), who also found a similar lack of support in the backbone of their tree which they attributed to a recent radiation in the group rather than limited or inadequate data, methodological artefacts or recurrent hybridization. The presence of African taxa at the base of most major clades provides evidence supporting a possible African origin with multiple - "Out Of Africa" events accounting for the diversity in the rest of the world. Evidence for the diversification of a single core African clade is lacking. The data suggest a more complex biogeographic history among the African members, with a large portion of the African diversity possibly arising through multiple, localized mini-diversifications.

2.4.1. The Physcomitrium lineage

Previous work on *Physcomitrium* and *Physcomitrella* (Liu et al., 2012; McDaniel et al., 2010) are in congruence with the phylogenetic relationships presented here. *Entosthodon hungaricus* is the only species of *Entosthodon* resolved within the *Physcomitrium* complex. A single character – the rostrate operculum - clearly ties *E. hungaricus* to *Physcomitrium* whilst its oblong exothecial cells, peristome teeth and lack of a complex revoluble annulus clearly tie it to *Entosthodon*. If further studies show that it belongs to an early lineage within *Physcomitrium*, retention of ancestral states might explain the strange combination of character states in *E. hungaricus*. It is also well known that members of the Funariaceae have the ability to form inter-generic hybrids (v. Wettstein, 1924) and it has repeatedly been hypothesized that hybridization could be an important speciation mechanism in the family. McDaniel et al. (2010), in their work on the *Physcomitrium-Physcomitrella* complex, provide evidence suggesting that *P. eurystomum* was formed from a hybridization event between two early diverging lineages of *P. sphaericum* and *P. pyriforme*. Morphologically, *E. hungaricus* shares charac-

teristics of both the genus *Physcomitrium* and *Entosthodon* and may represent a further case of speciation through hybridization. In the case of *E. hungaricus* the maternal parent would presumably be a *Physcomitrium*, since only these lineages are represented in the cp-DNA phylogeny, and the paternal parent an *Entosthodon*. Nuclear data could be more revealing on the issue by helping to identify any possible signatures of introgressive hybridization (McDaniel et al., 2010).

2.4.2. Entosthodon I

The species of this clade are largely from either Mediterranean or sub-tropical climates in the Southern Hemisphere and only *Funariella curviseta* is from the Northern Hemisphere. The eight African species are all endemic to the region and make up more than half of the known diversity in the clade. The African species represent mostly basal divergences in the lineage while the extra-African species tend to occupy crown positions. Interestingly, the African species appear to occupy different climatic regions within southern Africa and only two species, *E. succuleatus* and *F. sebapala*, share a similar high elevation environment in the Drakensberg Mountains of Lesotho. Biogeographically, this clade could have originated in the Southern Hemisphere given the lack of representation of species from the Northern Hemisphere. Additionally, the considerable diversity of African species in the clade suggests an African origin, a hypothesis that I aim to test explicitly in Chapter 4.

The clade, comprising mostly species of *Entosthodon sensu* Fife (1985), is punctuated by the presence of two monotypic genera, *Funariella* and *Physcomitrellopsis*. *Physcomitrellopsis* is morphologically distinct among other members of the clade due to its papillose calyptra and as its name implies, its morphological similarity to the genus *Physcomitrella* i.e. having immersed, cleistocarpic

capsules. As the phylogenetic position of *Cygnicollum immersum* Fife & Magill is unknown, *Physcomitrellopsis africana* is the only species confirmed from outside of the Physcomitrium clade bearing a similarly reduced sporophyte. McDaniel et al. (2010) previously demonstrated multiple independent origins of the genus *Physcomitrella* within the *Physcomitrium* complex, hence the possibility that transitions to a reduced phenotype may be more easily achievable than previously thought.

Funariella curviseta was originally segregated by Sérgio (1988) from *Entosthodon* based on morphological, karyological and phytogeographical differences from other members of the family. Upon inspection, however, the morphological differences of the taxon do not warrant its segregation from other members of *Entosthodon*. The spiral arrangement of cells of the operculum and the zygomorphic, inclined to pendulous capsule places the species within *E. subg. Plagiodus*, however, *F. curviseta* was considered to be divergent from *Entosthodon* because it lacked the double peristome of members of *E. subg. Plagiodus*. It is now apparent that the characters used to circumscribe the subgenera and sections are homoplasious. As shown below (Chapters 3 & 4), spirally arranged cells in the operculum are independent of capsule symmetry and are found both in species with zygomorphic capsules and in some with radially symmetric capsules. In the case of *F. curviseta* this hints at a recent loss of the peristome. Further, our limited understanding of karyological variation in the Funariaceae precludes its use as a taxonomic character. Morphologically, the species of Entosthodon I cannot be united by a single character alone. Species of this clade are generally larger on average than those of Entosthodon II and III and have reddish-brown rhizoids. The species *E. succuleata, P. africana, E. dixonii, E. balansae, E. smithhurstii, E. clavatus* and *E. apophysatus* are united by a unique combination of lightly papillose spores bearing trilete scars. Their spores are often thin-walled and are

usually collapsed when viewed under light microscope. The remaining species in the clade are also united by their spore ornamentation: all have distinct baculae (low rods or stubs) on the spore surface, a feature which is, however, not unique within Entosthodon I and is also observed in members of Entosthodon III. Sporophyte morphology within the clade is extremely variable even between sister species, varying from zygomorphic, peristomate capsules in *E. spathulatus* to radially symmetric and eperistomate capsules in *E. campylopodioides*.

2.4.3. Entosthodon II

The clade comprises seven species mostly of Northern Hemisphere distribution. *Entosthodon lindigii* and *E. jamesonii* were previously known only from South and Central America and Malesia (only *E. jamesonii*) and were recently shown to occur at high elevations in the Western Indian Ocean islands (Wilding and Hedderson, 2011), with *E. jamesonii* further known from Rwanda and Tanzania (Chapter 4). The Australian species *E. productus* is the closest relative of these two widespread species and the only species in Entosthodon II restricted to the Southern Hemisphere (Fife and Seppelt, 2001).

Again, no single morphological character unites all members of the clade. However, many share similar ovate or obovate to oblong-lanceolate leaves and often have peristomate capsules. *Entosthodon pulchellus, E. americanus* and *E. abramovae* all possess a unique combination of weakly dentate leaf margins, short conic opercula and two layers of peristome teeth and, together with *E. duriaei* and *E. jamesonii,* are among the few species known from calcareous substrates; the others are *Funariella curviseta* in Entosthodon I and *E. handelii* and *E. schimperi* in Entosthodon III. *Entosthodon productus*, *E. jamesonii* and *E. lindigii* were first recognized by Fife (1985; 1987), as closely related and are united by spores with trilete scars and verrucate (warty) to bullate (blistered or

puckered) surface ornamentation: this is the only group of species in the family to have spores with trilete scars apart from those species in Entosthodon I whose spores are lightly papillose.

2.4.4. Entosthodon III

The Rhomboideus clade comprises nine species of both Northern and Southern Hemisphere distributions. The Australian-Western European disjunct, *E. muhlenbergii*, is probably among the most well known species in the clade. It has been considered a close relative of *E. convexus* (Crundwell and Nyholm, 1974), which is supported here by their phylogenetic position. *Entosthodon rhomboideus* is the most well known of the three African species, which are all endemic to the region, occurring throughout the south-eastern parts of southern Africa while *E. lepervanchei* is known only from elevations above 1800 m on the Western Indian Ocean island of La Reunion and *E. claudineae* is known only from a few localities above 2000 m in the high mountains of Tanzania and Ethiopia.

Species of this clade all have well-developed, double peristomes and often posses bluntly dentate leaf margins. *Entosthodon lepervanchei* is the only species in the clade to possess strongly bordered leaves although the leaves of *E. claudineae* are at times bordered by a single row of narrower, elongate cells.

The Attenuatus clade comprises four species of both Northern or Southern Hemisphere distributions, including the type species of *Entosthodon, E. attenuatus*. Relationships between *E. attenuatus, E. obtusifolius* and a well supported clade comprising two African endemics, *E. pocsii* and *E. pertenellus* are unresolved.

Species in the Attenuatus clade are united by their upright, ± radially symmetric capsules and finely verrucate-lirate spores. Their leaves are often weakly

dentate in the upper half of the leaves. None of these characters are unique to the clade alone. The species share a similar climatic niche, occupying either high elevation tropical or temperate environments.

The Bergianus clade contains species from Africa, the Americas, Hawaii, Europe and Australasia. Five African species are spread throughout the clade, mostly of tropical or sub-tropical distribution, with the exception of *E. bergianus* and *E. limbatus* which occur in Mediterranean areas of the south-western Cape. The tropical species typically occur at elevations above 1000 m while the converse is true of the species from Mediterranean climates. On the whole, major relationships in the clade are well supported, and only the position of *E. laxus* remains unresolved along with a crown group polytomy. The species forming a polytomy are widely distributed in sub-tropical and tropical climates giving the group an almost pantropical representation. Branch lengths indicate a possible recent diversification into the tropics. *Entosthodon limbatus* is, however, present in both Mediterranean and temperate areas of South Africa and also in tropical habitats on Mauritius, and exemplars from each of these areas are present in the phylogeny. At this stage it is impossible to tell whether *E. limbatus* has a broad ecological niche or whether it consists of a number of cryptic species. The broad morphological diversity (discussed in more detail below) observed in the clade suggests recent dispersal and differentiation of lineages.

With the exception of *E. curvipes, E. radians* and *E. serratus* the species of the Bergianus clade typically have ± upright, radially-symmetric capsules. They are further united by having leaves that are often serrate and/or bordered in the upper ⅓–⅔ of the leaf. Short branch lengths are no indication of morphological diversity in the crown polytomy. Species belonging to this group display both peristomate and eperistomate capsules, leaves are bordered or not and capsules may, albeit infrequently, be zygomorphic.

2.4.5. Taxonomic considerations

Circumscription of the genera

Based on the present data, the current circumscription of *Entosthodon* cannot be retained without including *Aphanorrhegma, Bryobeckettia, Funariella, Loiseaubryum, Physcomitrium, Physcomitrella* and *Physcomitrellopsis*. Alternatively, it can be split into four segregate genera that maintain the criterion of monophyly (see Figure 2.2). I prefer this option as it better highlights morphological diversity in the group.

Entosthodon III is retained as *Entosthodon s.s.*, as it contains the type of the genus, *E. attenuatus*. For Entosthodon II I propose that the genus *Amphoritheca* be resurrected. Fife (1982) proposed that *E. lindigii* become the lectotype for *Entosthodon sect. Amphoritheca* because one was never designated by Hampe who originally erected the genus. In the case of the Dixonii clade, I propose the new generic name *Fifeobryum* N. Wilding to accommodate those species sister to *Physcomitrellopsis africana* but which lack immersed, cleistocarpic capsules. *Physcomitrellopsis* is retained as a monotypic genus because of its unique morphology amongst other members of *Entosthodon s.l.* (*Entosthodon s.l.* = Entosthodon I, II & III). The rest of Entosthodon I will fall under the next available name, *Funariella*.

Making new combinations under *Entosthodon* as well as any of the newly erected genera will be problematic in the absence of molecular data. Firstly, there has never been a comprehensive revision of the genus and much of the taxonomy remains in a state of chaos. Secondly, and more importantly, because of the pervasive homoplasy of morphological characters in the group there are few to no diagnostic characters that can be used to unambiguously circumscribe the genera. The majority of the taxonomic changes, including the description of new genera, will be addressed in Chapter 5.

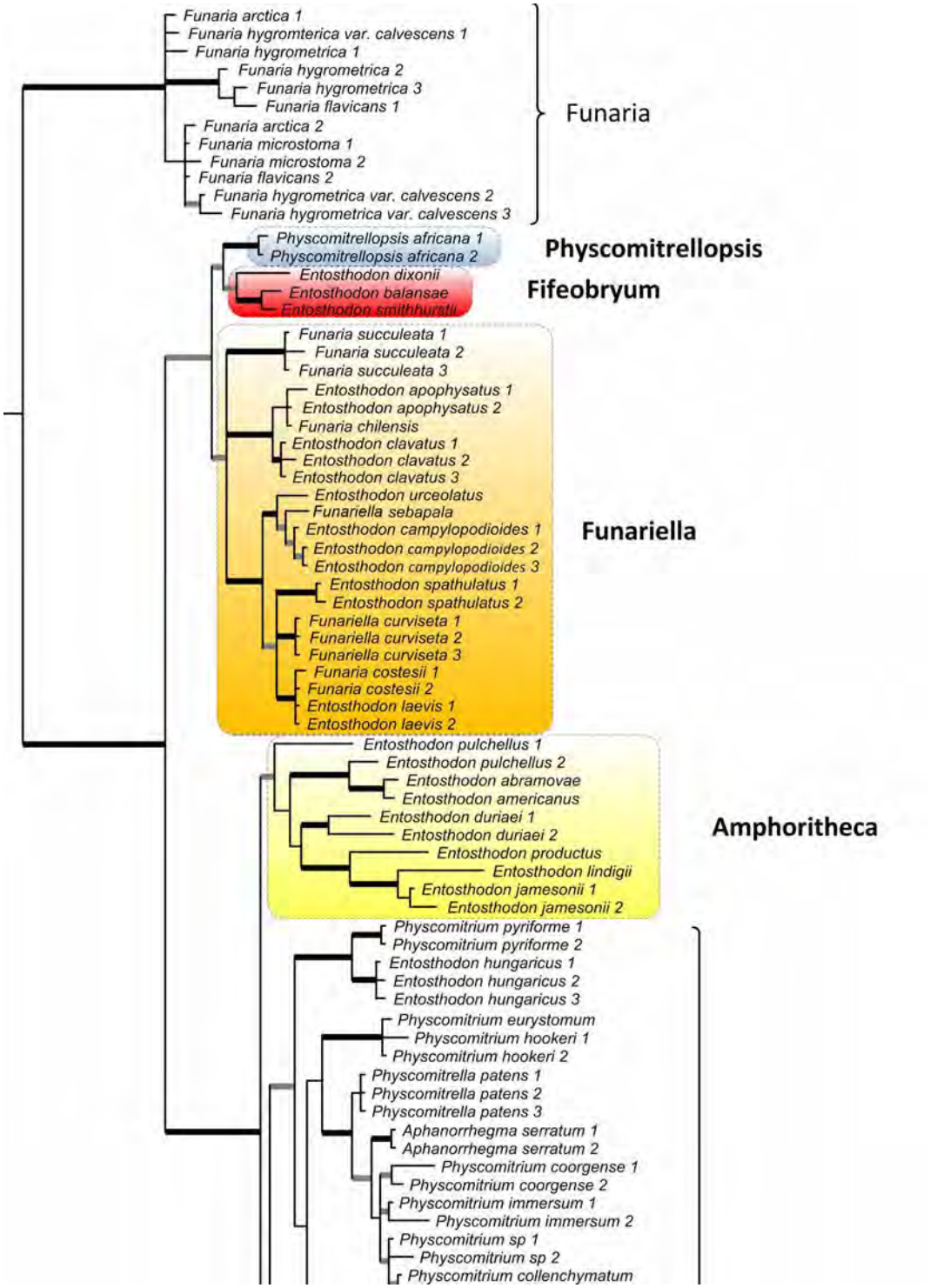

Figure 2.2: A proposed classification of *Entosthodon s.l.*. Figure continued on next page

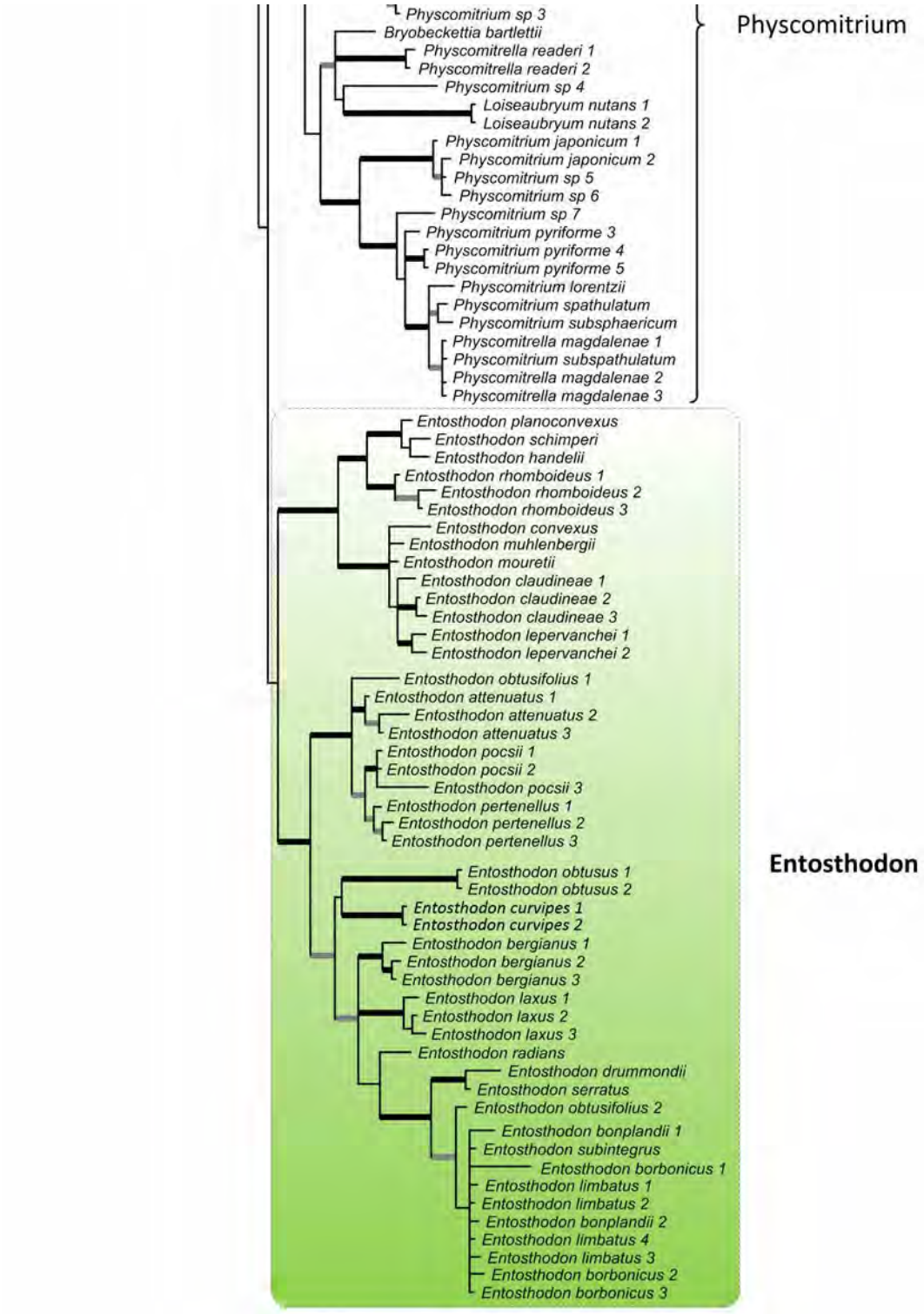

Figure 2.2: (continued)

2.4.6. Conclusions

The results presented here represent a major advance in the understanding of the evolutionary relationships within the Funariaceae and particularly *Entosthodon s.l.*. The genus itself is resolved in three main lineages with the African species spread amongst these. Future work should increase sampling of species and molecular data, in the hope that this will resolve key relationships along the backbone of the phylogeny. In particular the addition of nuclear markers should be used to test the validity of the new taxonomic changes, given the propensity for hybridization and reticulate relationships in the family.

The tree provides the basis for a revised classification of *Entosthodon* and a new circumscription of the genera. The *Entosthodon* lineages cannot easily be defined by a combination of character states because of the high levels of homoplasy in important taxonomic characters.

The multiple transitions to reduced sporophytic states provide an interesting back-drop to test hypotheses on the evolution of morphology in the group. In chapter 4, I reconstruct ancestral states in the Funarioideae sporophyte and provide tests of the order of character state evolution and whether these changes occur in a correlated fashion.

The origins of the African *Entosthodon* flora are complex, however, the basal positions of many African lineages suggests an African origin for possibly all of the major lineages. Whether the Northern hemisphere was colonized multiple times by African lineages is a possibility along with subsequent dispersal back into Africa. Thus the potential biogeographic scenarios accounting for the African species may be more complex than simple diversification of local lineages. In the next chapter (Chapter 3) I use the phylogeny presented here to address some of these questions explicitly.

2.5. Proposed nomenclatural changes in *Entosthodon s.l.*

Amphoritheca, Ann. Sci. Nat., Bot., Ser. 5, 3: 339 (1865).
Lectotype: *Amphoritheca lindigii* Hampe, Chapter 5.

Amphoritheca abramovae (Fedosov & Ignatova) N.Wilding comb. nov.
Basionym: *Entosthodon abramovae* Fedosov & Ignatov, Arctoa 19: 76 (2010).

Amphoritheca americana (Lindb.) N.Wilding comb. nov.
Basionym: *Funaria americana* Lindb., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 20: 398 (1863).

Amphoritheca duriaei (Schimp.) N.Wilding comb. nov.
Basionym: *Funaria duriaei* Schimp., Cat. Mous. Algérie 23 (1882).

Amphoritheca producta (Mitt.) N.Wilding comb. nov.
Basionym: *Entosthodon productus* Mitt., Fl. Tasman. 2: 197 (1859).

Amphoritheca pulchella (H. Philib.) N.Wilding comb. nov.
Basionym: *Funaria pulchella* H. Philib., Rev. Bryol. 11: 41 (1884).

Fifeobryum, gen. nov., Chapter 5.
Type species: *Fifeobryum longicollis* (Dix.) comb. nov.
Basionym: ***Funaria longicollis*** Dix., S. Afr. J. Sci. 18: 318 (1922).
The name *Entosthodon dixonii* was erected to accommodate *Funaria longicollis* under *Entosthodon* because of a conflict with an earlier homonym, *Entosthodon longicollis* Mitt.
Fifeobryum is named in honour of the bryologist Dr. Allan Fife whose taxonomic work and insights on the Funariaceae have opened up the family for many fields of research. A full description of the genus is presented in Chapter 5

Fifeobryum balansae (Besch.) N. Wilding comb. nov.
Basionym: *Entosthodon balansae* Besch., Mem. Soc. Nat. Sci. Natur. Cherbourg 21: 263 (1877).

Fifeobryum smithhurstii (Broth. et Geh.) N.Wilding comb. nov.
Basionym: *Funaria smithhurstii* Broth. et Geh., Oevf. Finska. Vetens. Soc. Foerh 37: 164 (1895).

Funariella apophysata (Tayl.) N. Wilding comb. nov.
Basionym: *Gymnostomum apophysatum* Tayl., London J. Bot. 5:43 (1846).

Funariella campylopodioides (Müll. Hal.) N.Wilding comb. nov.
Basionym: *Entosthodon campylopodioides* Müll. Hal., Hedwigia 38: 60. 1899.

Funariella chilensis (Thér.) N. Wilding comb. nov.
Basionym: *Funaria chilensis* Thér., Revista Chilena Hist. Nat. 30: 344. 25 f. 4 (1926).

Funariella clavata (Mitt.) N. Wilding comb. nov.
Basionym: *Funaria clavata* Mitt., Thes. Cap. 1: 63. pl. 100, f. B (1859).

Funariella costesii (Thér.) N.Wilding comb. nov.
Basionym: *Funaria costesii* Thér., Revista Chilena Hist. Nat. 25: 303. 27 f. 3 (1921).

Funariella laevis (Mitt.) N.Wilding comb. nov.
Basionym: *Funaria laevis* Mitt., J. Linn. Soc., Bot. 12: 248 (1869).

Funariella spathulata (Schimp. ex Müll. Hal.) N.Wilding comb. nov.
Basionym: *Funaria spathulata* Schimp ex Müll, Hedwigia 38: 61 (1899).

Funariella succuleata (Wager & C.H. Wright) N. Wilding comb. nov.

Basionym: *Physcomitrium succuleatum* Wager & C.H. Wright, Trans. Roy. Soc. S. Afr. 4: 3. pl. 1: D (1915).

Funariella urceolata (Mitt.) N. Wilding comb. nov.
Basionym: *Funaria urceolata* Mitt., Thes. Cap. 1: 63. pl. 100, f. C (1859).

Physcomitrium hungaricus (Boros) N. Wilding comb. nov.
Basionym: *Funaria hungarica* Boros, Magyar Bot. Lapok 23: 73 (1925).

3. Diversification of *Entosthodon s.l.* in space and time

3.1. Introduction

Understanding the process of diversification is one of the major goals of evolutionary biologists. Among the tools available, our ability to calibrate phylogenetic trees to absolute time and hence estimate dates of divergences (Drummond et al., 2006) is perhaps one of the most significant and exciting. Having an estimate of the absolute timescale over which a group has diversified allows us to make inferences about a number of variables that are thought to be relevant to the diversification process such as climate, geological context or whether the group underwent a rapid radiation. The literature abounds with studies documenting patterns of diversification in many different groups of organisms from birds (Barker et al., 2013) and plants (Richardson et al., 2001) to rotifers (Fontaneto et al., 2007) and bacteria (Stahl et al., 2002). The bryophytes have, however, received relatively little attention and dated phylogenies are few and far between. In a review of molecular clock calibrations and substitution rates in bryophytes (mosses, liverworts and hornworts), Villarreal and Renner (2014) counted a total of 17 studies, 8 on liverworts, 8 on mosses and 1 on hornworts. Considering that the bryophytes are the second largest group of land plants after the angiosperms, which comprise more than *ca*. 20 000 species (Magill, 2014) and lie at the heart

of understanding the transition to life on land, this is surprising. At the same time, bryophytes are significantly under-represented in the fossil record, because their fragile bodies do not form good fossils, which may make them less appealing for dating studies (Lacey, 1969). Mosses are particularly poorly represented in the fossil records of almost all geological periods (Frahm and Newton, 2005). The richest source of fossilized mosses (and liverworts) are those from Baltic and Dominican ambers (Frahm and Newton, 2005), but unfortunately taxonomic uncertainty is very high with moss amber fossils because they are often difficult to identify. While liverworts are typically complanate and can be viewed from both sides for identification, mosses are often spirally arranged meaning many of the important diagnostic features are obscured (Frahm and Newton, 2005). The lack of useful fossils for dating studies is evident in the literature and Villarreal and Renner (2014) found only a single study, by Aigoin et al. (2009), which used fossil mosses to calibrate their phylogeny. Accordingly, studies on mosses have largely relied on a combination of substitution rates derived from angiosperms and/or biogeographical events as calibrations, and these inevitably invoke a number of assumptions (Ho and Phillips, 2009). Many studies have cross-validated the different approaches (Bell et al., 2015; Feldberg et al., 2013; Wall, 2005; Aigoin et al., 2009; Pokorny et al., 2011; Huttunen et al., 2008; Nauheimer et al., 2012; Hartmann et al., 2006; Shaw et al., 2010) to determine congruence between alternative methods.

Substitution rates, although known to vary significantly among different lineages (Smith and Donoghue, 2008), show increasing evidence for applicability across a broad range of taxonomic groups. Recently, Villarreal and Renner (2014) obtained a substitution rate, *de novo*, of 5 x 10^{-4} from hornwort *rbc*l sequences, matching the rates used from angiosperm studies of 5 x 10^{-4} and further supporting the use of this substitution rate for bryophytes. Some uncertainty still remains

when using a common rate because cases are known where even sister species differ strongly in their mutation rates (Hedenäs, 2009).

Recent phylogenetic work on the Funariaceae points to the possibility that the family may have undergone a recent radiation. Liu et al. (2012) invoked this as an explanation after 10 loci failed to fully resolve relationships among the major lineages, i.e. those largely comprising members of *Entosthodon* and *Physcomitrium* among other smaller genera. To date, no studies have estimated divergence times within the family, although members of the Funariaceae have been included in other dating studies on mosses (Newton et al., 2007; Shaw et al., 2010). The first, by Newton et al. (2007), who dated the diversification of the pleurocarpous mosses using a penalized likelihood approach, estimated the age of the Funariidae at 187 Ma and the age of the Bryopsida at *ca*. 270 Ma. In contrast, Shaw et al. (2010) estimated the age of the Bryopsida at 209 Ma. The discrepancy between the two dates is not unusual, and studies using different datasets and implementing alternative methods have been known to produce estimates that differ significantly (Taylor and Berbee, 2006). These two studies suggest that the age of the Funariidae is likely to be younger than 200 Ma, bringing into question the affinity of possibly one of the oldest moss fossils, *Parafunaria sinensis*, which is dated at *ca*. 500 Ma, predating even our estimates of the divergence between the earliest moss and liverwort lineages (Rui-dong et al., 2004; Vanderpoorten and Goffinet, 2009). The age of this fossil and its taxonomic assignment are dubious and require further investigation.

The phylogenetic analyses presented in Chapter 2 show a paraphyletic *Entosthodon*, resolved into three major lineages (see Chapter 2, Figure 2.1). Based on these results, a revised classification was proposed (see Chapter 2, Figure 2.2) which I use here. The phylogenetic results from Chapter 2 suggest a complex biogeographic history within *Entosthodon s.l.*, with little geographic clustering ev-

ident among closely related species. Coupled with this is the similarly complex, and seemingly rapid, evolution of climatic niche.

For a long time it was believed that the distribution of many bryophyte taxa reflects ancient vicariance and that these taxa represented "unchanging sphinxes of the past" (Crum, 1972) with extremely slow rates of evolution. Biogeographical studies of bryophytes are now showing that divergence time estimates are generally not compatible with strict vicariance scenarios, concluding that long distance dispersal (LDD) is the best explanation for contemporary bryophyte distributions (Heinrichs et al., 2006; Muñoz et al., 2004; Hedderson and Zander, 2007b; Shaw et al., 2010). This is similarly supported by the presence of many widespread species on volcanic islands (Heinrichs et al., 2006; Wilding et al., 2013; Wilding and Hedderson, 2011). The ability of bryophytes to disperse over long distances is well established. The spore germination experiments of Van Zanten and Gradstein (1988) showed that spores of several liverwort species with intercontinental ranges could survive the conditions required to be successfully dispersed by trade winds. According to Van Zanten (1978) transequatorial transport of spores between the northern and southern hemispheres may be achieved by the Hadley circulation or by eddies in the upper troposphere for tropical and temperate species, respectively. Recent studies have conceived empirical tests of long distance dispersal, by wind (Muñoz et al., 2004) and by migratory birds (Lewis et al., 2014,?), demonstrating the functioning of such mechanisms in bryophytes.

Nonetheless, everything is not everywhere and most bryophytes still exhibit clear-cut ranges, suggesting that their distribution is not entirely stochastic as would be expected if LDD was commonplace (Feldberg et al., 2010; Heinrichs et al., 2006). Instead successful LDD may be the exception and short- to medium-range dispersal the norm. Molecular data provide growing evidence that no general biogeographic patterns exist in bryophytes, and scenarios differ on a case-

by-case basis (Heinrichs et al., 2006). By studying the biogeographic history of *Entosthodon s.l.* additional evidence can be brought to bear on this statement and add to the rapidly increasing literature on biogeographic patterns in these spore-dispersed plants.

Reconstructing the evolutionary history of a clade relies on our ability to infer the ancestral climates, geographical distribution of lineages and divergence times. Thus, using the most comprehensive phylogenetic tree of *Entosthodon s.l.* and the Funarioideae to date, this study aims to: (i) evaluate the effect of different calibration methods on estimates of divergence times in the Funarioideae. In the absence of fossil data for the Funariaceae, 3 alternative calibration methods are evaluated, 1) a secondary calibration from Newton et al (2007), 2) a rate of nucleotide substitution and, 3) the age of the Mediterranean type climates; (ii) using the time-calibrated phylogeny, evaluate the prediction that the Funarioideae have recently undergone a rapid radiation and, (iii) reconstruct ancestral biogeography and climatic niche in *Entosthodon s.l.* and use these data in conjunction with data from (i) to propose a hypothesis for the evolution and diversification of *Entosthodon s.l.* worldwide and to compare this to biogeographic patterns in other bryophyte groups.

3.2. Materials and Methods

3.2.1. Taxon sampling

The data set presented in Chapter 2 is used for all dating analyses. Additionally, *rps*4 accessions of *Encalypta ciliata* (genbank accession: AF223040) and *Bryobrittonia longipes* (genbank accession: JN088970) are included in the analyses as outgroups based on Newton et al. (2007). For the reconstruction of ancestral states the phylogenetic tree presented in Chapter 2 is used again but pruned so

that each species is present only once.

3.2.2. Molecular dating calibrations

The absence of the Funariaceae in the fossil record necessitates the use of alternative methods of calibration. Three of these are evaluated here. The first uses a normally distributed prior on the divergence time estimate for the Funariidae of 187 ± 23 Ma, published by Newton et al. (2007), as a secondary calibration. The use of secondary calibrations for phylogenies is generally not advocated because it is prone to significant error (Shaul and Graur, 2002; Graur and Martin, 2004). It has, however, been used by a number of studies (Gu, 1998; Wang et al., 1999; Hedges et al., 1996; Heckman et al., 2001; Moyle et al., 2012; Sauquet et al., 2012) and it is implemented here as one of few alternatives, and to provide a comparison to two additional methods of calibration. The second calibration method uses published cpDNA substitution rates. For this, a normal distribution with a mean of 5 x 10^{-4} substitutions per site per million years with a standard deviation of 1 x 10^{-4} was set as the prior distribution for substitution rate. This rate of substitution, although derived from tracheophyte coding sequences, has been shown to characterize a broader group of plants, including bryophytes (Villarreal and Renner, 2014). For the third calibration, the onset of Mediterranean-type climates is used to infer an age for the three species endemic to these areas. Contemporary Mediterranean climates formed within the last 10 million years. In the Southern hemisphere these seasonally dry regions are of approximately equal age: in Chile (7–9 Ma) and South Africa (6–10 Ma) (Siesser, 1980; Kleinert and Strecker, 2001; Linder, 2003), but of more recent origin, 3–5 Ma, in Australia (Hopper and Gioia, 2004). A clade comprising *Funariella clavata* of South Africa, sister to a clade comprising *E. chilensis* of Chile and *E. apophysatus* of South America and Australia form a clade that is entirely restricted to

arid Mediterranean type climates in the Southern hemisphere. These species, (see Chapters 2, 4 & 5) probably diversified into Mediterranean areas after their onset in the late Miocene-Pliocene. By using the age of Mediterranean systems a maximum age can be placed on species endemic to these regions, similar to what has been done for volcanic islands (e.g. Warren, 2003). Hence, a divergence time of 6–10 Ma, using a uniform prior distribution, is placed on the split between *F. clavata* and the sister pair *F. chilensis* and *F. apophysata*.

This method of calibration makes a number of biogeographic assumptions: i) that the species are truly endemic and do not occur elsewhere, ii) that the three species are each other's closest living relatives and iii) that dispersal or genetic divergence between the three regions occurred after the onset of a Mediterranean climate. Recent work on *Entosthodon s.l.* strongly supports the first two assumptions (see Chapters 2 & 5). The third assumption is supported by the fact that the drastic orographic, climatic and vegetation changes that took place (Kleinert and Strecker, 2001; Martin, 2006) during the Neogene, prior to the onset of Mediterranean climates in these areas, would have made it very unlikely that similar distributions could have existed at the time.

3.2.3. Divergence time estimation

Molecular dating was performed using a relaxed-clock Monte Carlo Markov Chain (MCMC) approach, applying an uncorrelated log-normal model of rate variation among branches and a Yule process prior for branching times, implemented in BEAST v 1.8.1 (Drummond et al., 2012) using the sequence data presented in Chapter 2. BEAST employs a flexible MCMC algorithm which jointly estimates species tree topology, divergence times, and population sizes from multiple embedded gene trees under the multispecies coalescent model. Parameters, including substitution rate were linked across the four cp-DNA loci (in line with

PartitionFinder (Lanfear et al., 2012) results from Chapter 2).

Tree topology was constrained in the BEAST analyses such that the monophyly of *Encalypta* and the Funarioideae was enforced in line with Newton et al. (2007). The best available phylogenetic hypothesis (Chapter 2) for the subfamily was used here to further constrain phylogenetic relationships in the BEAST analysis such that the same relationships between the major lineages were present in the time calibrated tree. This is also thought to speed up the time it takes for the analysis to reach convergence as it reduces the number of possible topologies that BEAST must integrate over.

All BEAST analyses were run on the CIPRES Science Gateway V3.3 (Miller et al., 2010). The MCMC chains were run for 80 million generations, with parameters sampled every 8000th generation. Random starting trees were used for all runs. Data were checked for 'clockliness' using the ucld.stdev parameter (Drummond & Ho 2007). The effect of the priors was assessed by running an analysis with an empty alignment which sampled only from the prior. Tracer 1.5 (part of the BEAST package) was used to assess effective sample sizes (ESS) for all estimated parameters and to judge the percentage of burn-in for tree constructions. Two runs were performed for each analysis and independent runs were combined using logcombiner (part of the BEAST package). Trees were combined in TreeAnnotator 1.7.5 (part of the BEAST package), and maximum clade credibility trees with mean node heights were visualized using FigTree 1.4.0 (Rambaut, 2007). Highest posterior densities (HPD) intervals (the interval containing 95 % of the sampled values) are reported for key nodes.

3.2.4. Scoring of characters

Climate type and ecozone were scored (see Appendix A, Table A.2) for each species based on information in the literature and from herbarium specimens.

Broad biogeographic zones are considered to be the most appropriate scale for the purpose of determining the geographic origins of the different lineages since this best reflects the scale of species distributions. Ecozone was determined according to Udvardy (1975) and climate type according to the Köppen-Geiger climate classification (Kottek et al., 2006). Where species occurred in more than one biogeographic zone or climatic zone these were scored as having multiple equally plausible states. Temperate climates were divided into temperate oceanic and temperate steppe because this difference better reflected the distribution of many species and no species were common to both climate types. For the purpose of the analyses the Hawaiian species, *E. subintegrus*, was coded as falling within the Nearctic zone.

3.2.5. Reconstruction of ancestral states

By using a Bayesian approach to character evolution, uncertainties in topological relationships and evolutionary distances can be accommodated among nodes and species when inferring ancestral states. The BI approach used the 'Multistate' option in BayesTraits v2.0 (Pagel and Meade, 2006) on a set of 4500 trees generated by BI in MrBayes (Ronquist and Huelsenbeck, 2003) (see Chapter 2). BayesTraits has the advantage of being able to test numerous models by employing a reversible jump (RJ) MCMC which searches the posterior distribution of different models of evolution as well as the posterior distributions of the parameters of these models. Ancestral states were reconstructed for ten key nodes using a RJ hyperprior (RJHP), with an exponential prior seeded from a uniform distribution on the interval 0–10. A hyperprior is simply a distribution, usually uniform, from which values are drawn to seed the values of the exponential gamma priors. Hyperpriors provide an elegant way of reducing some of the uncertainty and arbitrariness associated with choosing priors in MCMC analyses (Pagel and Meade,

2006). The AutoTune option was used to find an optimal RateDev parameter. Analyses converged after 10 million generations and a burnin of 10 percent was used.

3.2.6. Diversification analyses

BAMM (Bayesian analysis of macroevolutionary mixtures) tools (Rabosky et al., 2014), an R package for the analysis and visualization of evolutionary dynamics was used to estimate net diversification rates across the Funarioideae tree. BAMM runs on a Bayesian framework that uses reversible-jump MCMC to explore a vast state space of candidate diversification models and explicitly accommodate diversification rate variation through time and among lineages.

3.3. Results

3.3.1. Dating analyses

A lognormal relaxed clock fitted the data better than a strict clock. Clockliness was checked by examining the coefficient of variation parameter under a relaxed clock model. Values close to 0 indicated that the data have evolved in a clock-like manner.

Table 3.1 summarizes age estimates for selected clades for the different calibration methods. The use of a secondary calibration from Newton et al. (2007) yielded divergence estimates that are substantially older than those resulting from the calibration methods using either substitution rate or the age of the Mediterranean climates. Ages derived from the latter two methods are more similar and are considered to provide a better estimate of divergence times. Divergence times inferred using the age of Mediterranean climates are on average about 50 % older than those inferred based on a fixed substitution rate, while those inferred using

a secondary calibration are in excess of 300 % greater than divergence estimates inferred using a substitution rate. The combination of the two preferred calibration methods (i.e. not the secondary calibration) yielded divergence time estimates that are very similar to those from the use of substitution rate alone, with the exception of the calibrated node. The use of a fixed substitution rate yielded the tightest 95 % HPD of the three methods. The calibration using the age of Mediterranean climates yielded the widest 95 % HPD of the three methods near the root of the tree. Apart from the root, the overall width of the 95 % HPD were comparable between the latter two methods.

Table 3.1: Estimated divergence times of critical nodes in the phylogeny of the Funarioideae using four different calibration methods in a Bayesian molecular dating framework: (i) the root age was constrained to a mean of 187 Ma with a standard deviation of 9.8 (corresponding the mode and 95 % HPD for the tmrca of the Funariidae in Newton et al. (2007), (ii) an overall average rate of substitution, (iii) a constraint on the age of the Cape endemic *F. clavata* was set to 8 Ma with a standard deviation of 0.78 Ma to account for uncertainty around the age of the Mediterranean climate in the Cape of South Africa, (iv) a combination of constraints ii and iii, further displayed in Figure 3.1

Node	Clade Age (Ma)							
	Root		Substitution rate (SR)		Clavata (CL)		Combined (CL - SR)	
	Mean	95 % HPD	Mean	95 % HPD	Mean	95 % HPD	Mean	95 % HPD
1	184.5	155.7–216.2	52.5	39.1–67.7	76.2	23.6–144.2	51.8	38.1–66.2
2	172.0	154.2–189.5	48.6	36.7–61.5	76.7	23.2–133	47.9	36.6–59.8
3	113.6	91.6–138.6	33.8	25.7–42.8	48.8	18.3–90.	33.8	25.9–42.8
4	105.1	80.6–128.7	31	24.2–38.9	44.9	17.6–84.2	31.1	23.6–38.5
5	63.6	38.9–86.5	18.8	12–25.7	27.5	10.1–51.6	19.4	12.6–26.5
6	17.4	6.2–32.3	5.5	2–10.1	7.8	6.3–9.4	7.7	6.1–9.1
7	83.3	60.6–105.4	25	19.5–30.7	36.5	13.9–68.3	25.4	20.1–31.4
8	70.4	48–92.8	20.9	14.7–27	30.5	10.8–57.1	21.2	14.9–27.1
9	80.1	58.6–102.5	24	18.6–29.4	35.1	11.8–64.5	24.3	19.1–30
10	66.5	44.1–88.6	19.9	14–25.6	29.1	9.8–54	20.1	14.4–25.9
11	73.8	52.4–94.3	22.1	17.1–27.4	32.3	11.1–59.3	22.3	17.1–27.6
12	47.6	28.6–67.8	14.5	9.4–20	21.3	7.3–41	14.7	9.5–20.4
13	60.7	42.4–81.2	18.1	13.6–23.4	26.3	9.3–49.8	18.2	13.4–23.2
14	18.6	10.3–28.3	5.7	3.3–8.4	8.3	2.3–16.1	5.8	3.3–8.5
15	47.5	26.9–71.9	14.9	8.5–22.1	22	6.5–42.9	15.1	8.6–22.1

A dated tree employing the two calibration methods yielding the most congruent divergence time estimates is presented in Figure 3.1. With the exception of a few terminal taxa, the BEAST analysis, as expected, produced a very similar topology to the MrBayes tree shown in Chapter 2 and used here for the reconstruction of ancestral states. The tmrca of the Funarioideae is estimated at 51 Ma (38.1–66.2: 95 % HPD). The diversification of *Entosthodon s.l.* began 31.1 Ma during the Middle Oligocene and by the Early Miocene all three main lineages of *Entosthodon s.l.* are present. The ages of the MRCA of the extant members of the Funariella-Physcomitrellopsis clade, *Amphoritheca* and *Entosthodon s.s.* are estimated at respectively 19.4 Ma, 21.2 Ma and 22.3 Ma (see Table 3.1 & Figure 3.1).

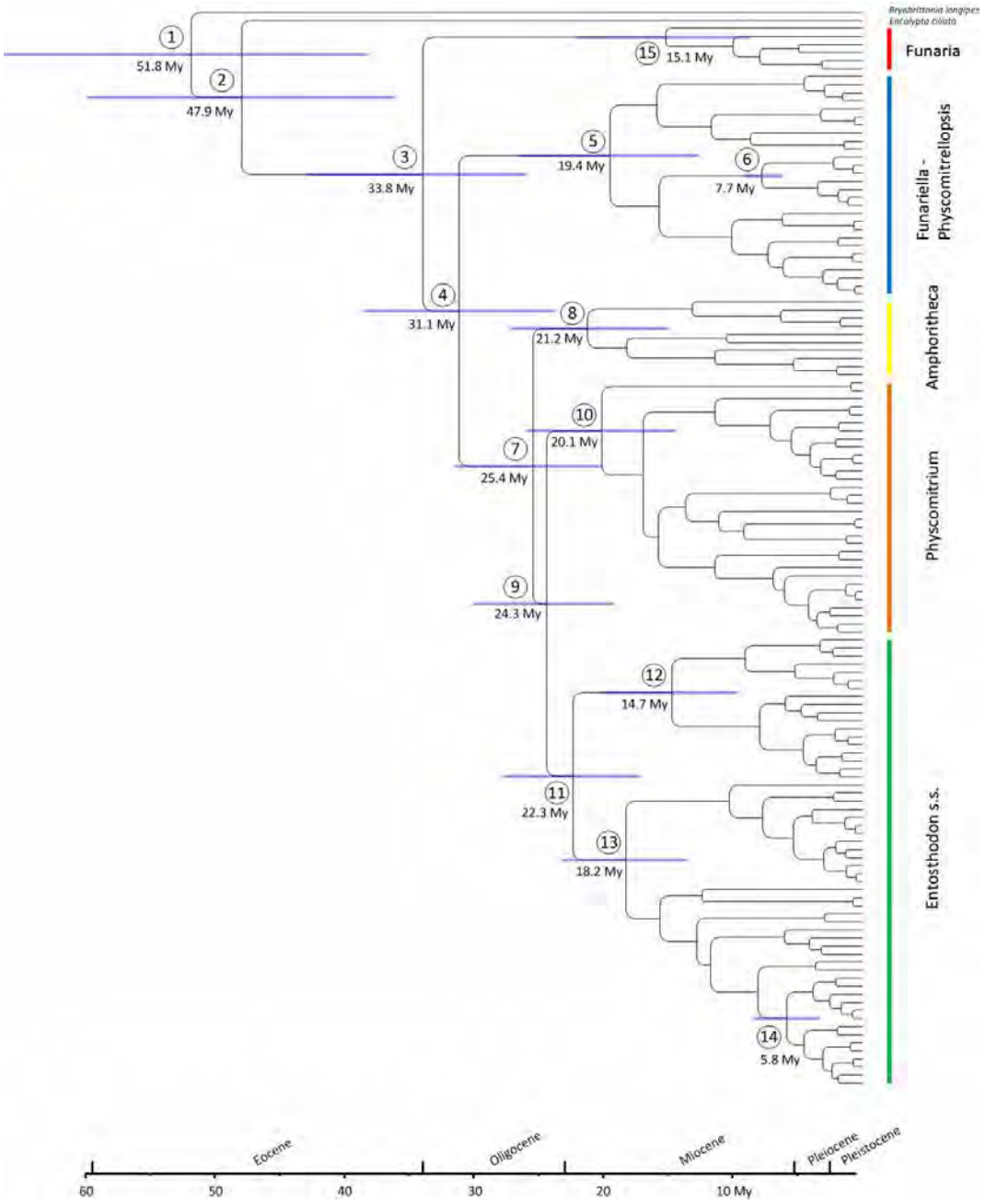

Figure 3.1: Chronogram of the Funarioideae based on the cpDNA dataset presented in Chapter 2 and inferred using BEAST. Two methods were used to calibrate the tree: i) an overall prior constraint on substitution rates and, ii) a constraint on the age of the Mediterranean climates in Chile and South Africa. The calibration point is node no. 6 on the chronogram. Blue bars represent the highest posterior density credibility interval for node ages. Estimated divergence times appear below nodes 1-15 and in Table 3.1.

3.3.2. Diversification analysis

The BAMM analyses ran on a set of 4000 calibrated trees resulting from the BEAST analysis. Net diversification rate was estimated at 0.12 species per Ma for the Funariella-Physcomitrellopsis clade and *Amphoritheca* and 0.13 species per Ma for *Entosthodon s.s.*. Figure 3.2 shows the net diversification rate across the Funarioideae tree. The overall trend, in all but *Funaria*, is an increase in diversification rates towards the present.

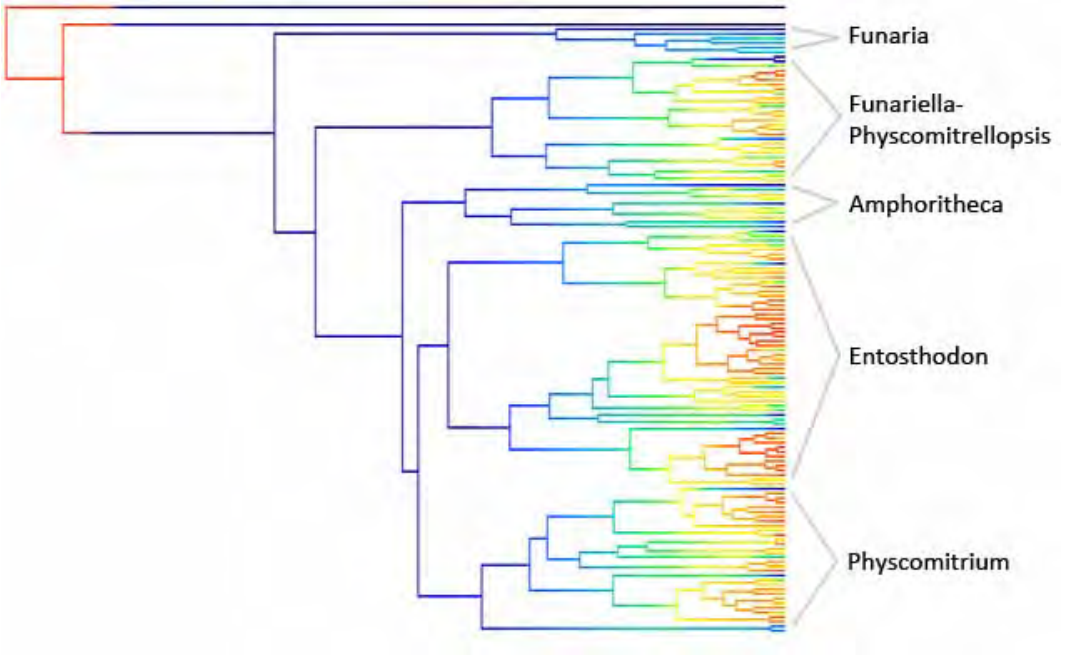

Figure 3.2: Chronogram showing the results of the BAMM diversification analysis. Net diversification rate is represented by colour. Cool colours represent slower diversification while warm colours indicate an increase in the net diversification rate. Colour mapping is determined by binning the results of the BAMM analysis.

3.3.3. Ancestral reconstructions of biogeography and climatic niche

The reconstructions indicate (Figure 3.3) that the Funariella-Physcomitrellopsis clade probably originated in temperate steppe climates in Africa during the early Miocene, 19.4 Ma (12.6–26.5: 95 % HPD; Figure 3.1). The appearance of open, C4 grass-dominated habitats in Africa during the Middle to late Miocene (Strömberg, 2011) supports the presence of a temperate steppe climate at the time. The clade diversified largely into temperate steppe and Mediterranean climates in the Southern Hemisphere with two independent transitions into areas with tropical climates

The MRCA of *Amphoritheca* is reconstructed (Figure 3.4) as being from Mediterranean climates in the Palearctic during the early Miocene, 21.2 Ma (14.9–27.1: 95 % HPD) although support for an ancestor from temperate oceanic areas of the Palearctic is almost equivocal. Shifts into temperate oceanic and steppe climates as well as tropical occurred during the middle to late Miocene.

The ancestor of *Entosthodon s.s* is reconstructed as occurring in tropical climates in the Afrotropics, 24.3 Ma (19.1–30: 95 % HPD) and with the exception of the rhomboideus clade, almost identical reconstructions are present throughout the rest of *Entosthodon s.s.*. The MRCA of the rhomboideus clade of *Entosthodon s.s.* is reconstructed from Mediterranean climates in the Palearctic, 14.7 Ma (9.5–20.4: 95 % HPD). The rhomboideus clade diversified largely into Mediterranean areas of the Palearctic during the Middle miocene but made multiple transitions into temperate climates and one transition back into tropical climates. The MRCA of the attenuatus clade is reconstructed from tropical climates in the Afrotropics during the Middle to late Miocene (13.4–23.2 95 % HPD). The attenuatus clade diversified mainly in tropical areas of the Southern Hemisphere.

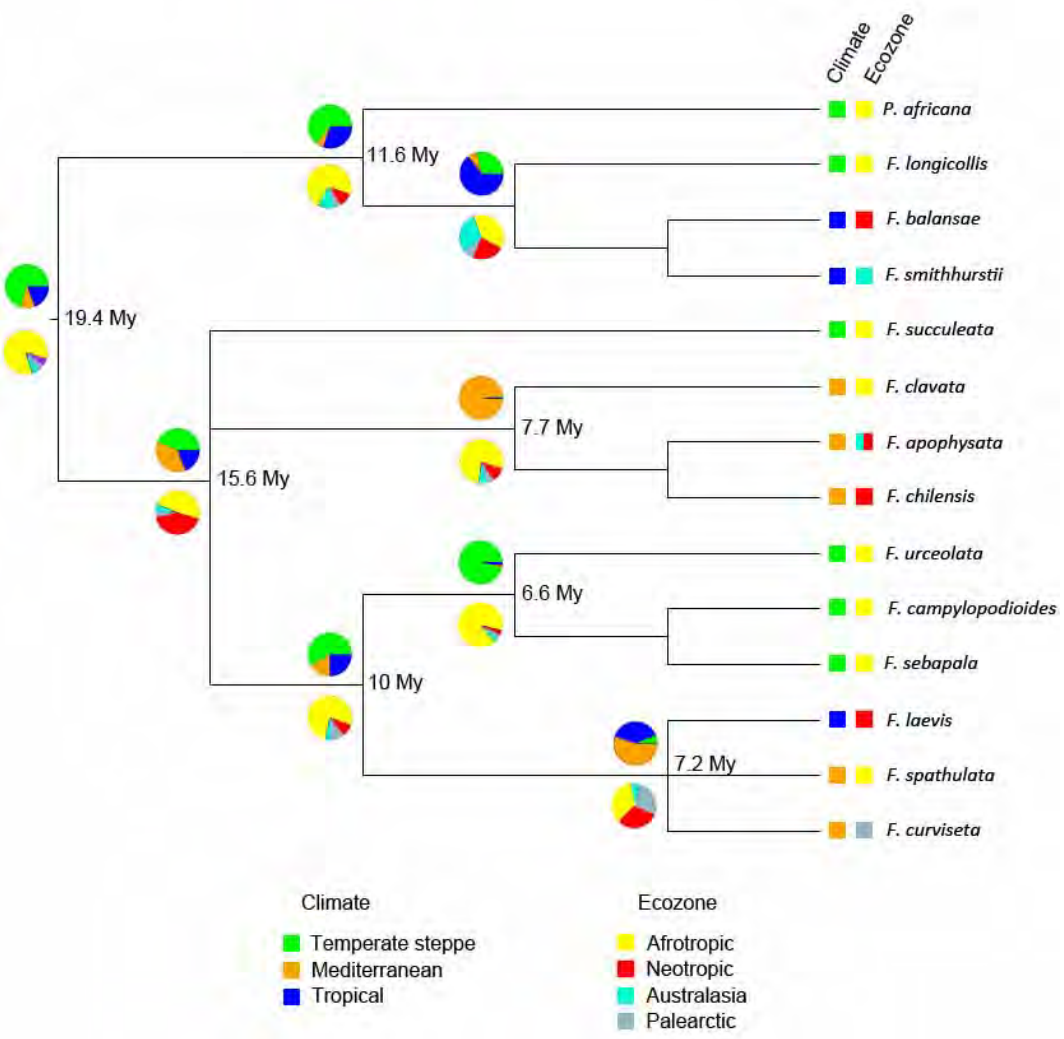

Figure 3.3: Bayesian reconstruction of ancestral climatic niche and ecozone in the Funariella-Physcomitrellopsis clade. Pie charts represent the most likely reconstruction of ancestral climate (top pie) and ecozone (bottom pie). The ages of selected lineages are indicated at the relevant nodes along the cladogram.

The ancestral, tropical climatic niche was mostly retained in the attenuatus clade with most transitions occurring into temperate oceanic climates and only one into a Mediterranean climate.

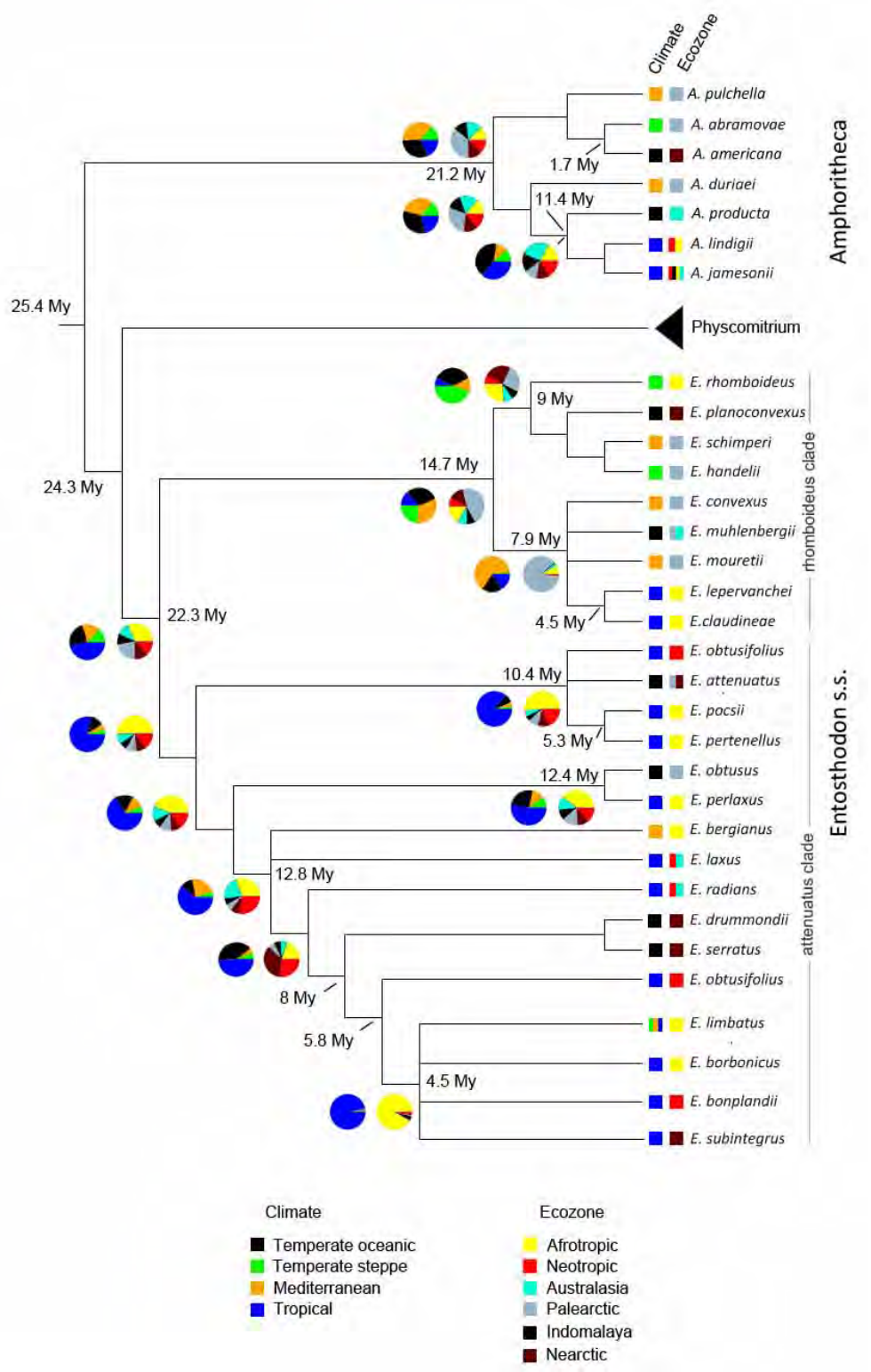

Figure 3.4: Bayesian reconstruction of ancestral climatic niche and ecozone in *Amphoritheca* and *Entosthodon s.s.*. Pie charts represent the most likely reconstruction of ancestral climate (left pie) and ecozone (right pie). The ages of selected lineages are indicated at the relevant nodes along the cladogram.

3.4. Discussion

3.4.1. Calibration methods

The lack of congruence between the three calibration methods was not unexpected. The close correspondence between divergence estimates inferred using a fixed substitution rate and those inferred using the age of Mediterranean climates suggests that these methods might provide a more accurate estimate of divergence times in the Funarioideae. The use of the secondary calibration from Newton et al. (2007) results in divergence estimates across the Funarioideae tree that are *ca*. 2–3 times older than those obtained using the other calibration methods. Bryophyte dating studies may all use the same root calibration of 450 Ma (Newton et al., 2007; Shaw et al., 2010), corresponding to the age of the earliest bryophyte fossil, however, they obtain vastly different age estimates probably because of differences in methodology and data. The use of secondary calibrations is generally not recommended as they are prone to propagating significant error within subsequent dating analyses, especially if there are biases in the original analysis that are not taken into account (Graur and Martin, 2004).

The presence of oceanic island endemics provides a means of cross validating dating estimates. The combination of the two preferred calibration methods yields a divergence time of 3.5 Ma (1.4–6.2: 95 % hpd) for the age of the Réunion island endemic, *E. lepervanchei* Besch., and its sister species, *E. claudineae* Wilding, in East Africa. The divergence estimate overlaps with the age of the island which is estimated at 1.91–2.1 Ma (McDougall and Chamalaun, 1969) lending support to the divergence time estimates inferred using the substitution rates and the age of Mediterranean climates.

3.4.2. Evidence of a recent and rapid radiation

The diversification rates recovered here for *Entosthodon s.l.* are equivalent to mean diversification rates in angiosperms (Stenøien, 2008; Eriksson and Bremer, 1992) and are among some of the fastest rates recorded for bryophytes, confirming earlier suspicions of a rapid radiation in the group (Liu et al., 2012). Radiations within moss lineages are typically nowhere near as spectacular as in the angiosperms (Hughes and Eastwood, 2006). Average rates of diversification for the bryophytes are shown to be in the range of between 0.015 and 0.026 but as high as 0.18 species per Ma in rapidly diversifying groups such as Ricciaceae (Laenen et al., 2014). Two of the fastest radiations in the bryophytes are in the tropical moss *Mitthyridium* which diversified at a rate of 0.56 (0.556–0.564) species per Ma (Wall, 2005) and *Homalothecium* at 0.5 (0.28–1.0) species per Ma (Huttunen et al., 2008), equivalent to some rapid angiosperm radiations like the adaptive radiation of Hawaiian Silverswords (Baldwin and Sanderson, 1998), which diversified at a rate of 0.56 ± 0.17 species per Ma and the southern African Aizoaceae (Klak et al., 2003), which diversified at a rate of 0.77-1.75 species per Ma. According to Shaw (2010), diversification of Peat mosses, which number between 300 and 500 species globally, occurred within the last 20 Ma and though no diversification rates have been calculated for the group the diversification of peat mosses could turn out to be one of the most rapid radiations in the bryophytes.

The rapid diversification of *Entosthodon s.l.* is evident both at a molecular level and at a morphological level. The lack of resolution along the backbone of the Funariaceae phylogeny provided the first evidence that the *Entosthodon s.l.* and *Physcomitrium s.l.* could have undergone a recent and rapid radiation (Liu et al., 2012). Morphologically, these same lineages are plagued by homoplasy and an almost complete lack of unique characters. Searching for correlates of diversification in the group is clearly the next step in unravelling how and

why the group has diversified so rapidly. In particular, a better understanding of morphological evolution will help to determine whether signatures of adaptation exist and whether certain characters and their role in the diversification of the subfamily warrant further investigation.

3.4.3. African origins and diversification of *Entosthodon s.l.*

The biogeographic history of *Entosthodon s.l.* is complex, involving multiple dispersals within and between both Northern and Southern Hemispheres. However, when compared to biogeographic patterns displayed in other bryophyte groups the situation in *Entosthodon s.l.* is not unusual. The biogeographic structure observed in *Entosthodon s.l.* has undoubtedly, to a significant extent, been influenced by their ability to disperse over long distances. Dispersal in the genus was likely facilitated by their wind dispersed spores and the ability of the monoecious plants to easily self-fertilize and establish populations.

The relatively young age of the three main *Entosthodon s.l.* lineages refutes a Gondwanan hypothesis or other diversification scenarios invoking ancient vicariance, suggesting that the distribution of *Entosthodon s.l.* is the result of LDD alone. Indeed, this is supported by recent studies which show that dispersal usually provides a better explanation of bryophyte biogeography (Shaw et al., 2008; Feldberg et al., 2006). In some cases studies still support Gondwanan or Laurasian origins (Blöcher, 2004; Feldberg et al., 2010; Heinrichs et al., 2006; Feldberg et al., 2007, 2006), but these typically lack a dating approach making their hypotheses impossible to validate.

The Funariella-Physcomitrellopsis clade diverged from *Amphoritheca, Entosthodon s.s.*and the Physcomitrium lineage 31.1 (23.6–38.5: 95 % HPD) Ma. The Funariella-Physcomitrellopsis clade probably originated in southern Africa during the early Miocene, 19.4 (12.6–26.5: 95 % HPD) Ma, where it still main-

tains most of its diversity today. The group made a number of dispersals into the Neotropics and possibly Australasia during the Middle Miocene, and one recent dispersal into Europe from Africa or the Neotropics, 7.2 (3.7–11.1: 95 % HPD) Ma. As is suggested by the presence of only one disjunct species in the Funariella-Physcomitrellopsis clade, dispersal must have been followed by genetic divergence.

Amphoritheca diverged from *Entosthodon s.s.* and the Physcomitrium lineage 25.4 (20.1–31.4: 95 % HPD) Ma in the late Oligocene-Early Miocene. The origin of the lineage is reconstructed as Palearctic 21.2 (14.9–27.1: 95 % HPD)Ma, making it the only lineage with a Palearctic origin. *Amphoritheca* diversified largely in Europe, dispersing once into the Nearctic and probably once into the Southern Hemisphere.

Entosthodon s.s., the largest lineage, is reconstructed as having its MRCA in Africa, 22.3 (17.1–27.6: 95 % HPD) Ma. The rhomboideus clade appears to have dispersed to Europe between 14.7 (9.5–20.4: 95 % HPD) Ma and 22.3 (17.1–27.6: 95 % HPD) Ma where it subsequently diversified into a recently opened climatic niche (discussed below). Members of this clade dispersed into the Nearctic, Africa and Australasia within the past 10 Ma. The attenuatus clade diversified mainly in Africa and the Southern Hemisphere. Members of the clade dispersed multiple times into the Nearctic, Palearctic, Neotropics and possibly Australia. Some dispersal events were followed by genetic divergence and speciation while a number of other species were able to maintain disjunct distributions. What allows certain species to successfully maintain such wide distributions while others quickly diverge and form new species is an interesting question lying at the heart of biogeography. Clearly, in *Entosthodon s.s.*, it is not spore size which determines this alone, as spore size is roughly equivalent in the three lineages of *Entosthodon s.l.* (Fife, 1985, 1982, Chapter 5).

3.4.4. Biogeographic patterns and dispersal routes

Southern Hemisphere

Southern Hemisphere biogeography of *Entosthodon s.l.* is characterized by two important patterns of shared ancestry, i) Africa - Neotropics and ii) Neotropics - Australasia. The latter two areas often share species, as is the case for *Amphoritheca jamesonii, Funariella apophysata, Entosthodon laxus* and *Entosthodon radians*, or have species which have their closest relative in the other area, such as the species pair *Fifeobryum balansae* and *Fifeobryum smithhurstii*. Similarities between the angiosperm floras of Australia and South America have long been recognized. Sanmartín et al. (2007) assessed dispersal asymmetries between Australia and South America and found that Eastward dispersal from Australia occurred more frequently than dispersal in the opposite direction. As is shown here for *Entosthodon s.l.*, dispersal between the Neotropics and Australasia during the Middle to Early Miocene has also been shown for Hornworts (Villarreal and Renner, 2014).

The Neotropical-African disjunction is especially common in mosses. The Neotropical flora shares with Africa about 334 specific and infraspecific moss taxa (Delgadillo, 1993). *Amphoritheca lindigii* is the only species in *Entosthodon s.l.* restricted to the Neotropics and Africa. Its sister species, *A. jamesonii*, occurs in Africa, the neotropics, Australasia and Indomalaya. Evidence from the reconstruction of ancestral areas suggests that dispersal via the Neotropics may be an important migration route into Australasia for species of *Entosthodon s.l.*. In clades which are reconstructed with an African origin, species with Australasian distributions are either disjunct in the neotropics or have a sister species in the neotropics but never the other way around. This suggests that the Neotropics may be an important stepping stone into Australasia for species dispersing from south-

ern Africa. Numerous examples of transoceanic dispersal between Australasia, the Neotropics and Africa are known in bryophytes (Shaw et al., 2008; Feldberg et al., 2010; Heinrichs et al., 2009; Feldberg et al., 2006; Delgadillo, 1993), pteridophytes (Kreier and Schneider, 2006; Moran and Smith, 2001) and angiosperms (Dick et al., 2007; Michalak et al., 2010; Renner, 2004b; Liu et al., 2013; Nylinder et al., 2013; Givnish and Renner, 2004) although the predominant mode of dispersal in angiosperms is more commonly transportation by oceanic currents rather than by wind (Renner, 2004a).

Northern Hemisphere

Dispersal within the Northern Hemisphere occurred primarily between the Palearctic and the Nearctic, i.e. Western Europe–Western North America. This biogeographic pattern has been documented in many plant groups and Schofield (1988) and Schofield and Crum (1972) recognized it as one of two major bryophyte biogeographic patterns in the Northern Hemisphere. Sixty-five percent of all mosses in North America are also found in Europe (Frahm and Vitt, 1993). In comparison, only 6.5 % of the vascular flora is shared between North America and Europe (Qian, 1999). A number of mechanisms have been proposed to account for amphi-atlantic and Western Europe–Western North America disjunctions including dispersal via the North Atlantic Land bridge during the early Tertiary, dispersal via the Bering land bridge from the early Palaeogene into the late Miocene/early Pliocene (Milne, 2006), and long distance dispersal across the Atlantic or Pacific Ocean (Emadzade and Hörandl, 2011). These scenarios are clearly more applicable to plants exhibiting older divergences. Divergence times in *Entosthodon s.l.* suggest recent Pliocene dispersal across the Atlantic. According to the estimates trans-Atlantic dispersal occurred twice within the last 3.2 Ma, always from Europe into North America. Examples of dispersal in ei-

ther direction have been recorded in bryophytes (Stenøien et al., 2011; Fuselier et al., 2009). However, Szövényi et al. (2008) found a pronounced skew in trans-Atlantic migration patterns in six *Sphagnum* species, with ongoing and historical migration being greatest from Europe towards North America. The common ancestor of *Amphoritheca abramovae* and *Amphoritheca americana* crossed the Atlantic around 1.7 Ma (0.13–4.0: 95 % HPD) while the ancestor of *E. planoconvexus* and *E. schimperi* dispersed out of Europe within the last 3.2 Ma (0.85–6.4: 95 % HPD). Clearly these dates are not congruent with either land bridge hypothesis.

Inter-Hemisphere dispersal

Inter-Hemisphere dispersal in *Entosthodon s.l.* occurs most often from the Southern to Northern Hemisphere. Seven potential dispersals occurred into the Northern Hemisphere and only three into the Southern Hemisphere. Disjunctions spanning both hemispheres are fairly common in bryophytes. These include the amphitropical disjuncts (Lewis et al., 2014), which are among the most well documented of such patterns in plants generally (Wen and Ickert-Bond, 2009), pantropical disjuncts (Goffinet and Shaw, 2009), and bipolar disjuncts (Ochyra et al., 2008).

In *Entosthodon s.l.*, the most common dispersal scenario out of the South is from Africa or South America into the Palearctic or Nearctic. The origin of a few of these dispersals is obscured because of a lack of resolution in the phylogeny or because of equivocal probabilities in the reconstructions. It is clear though that the ancestor of *Entosthodon obtusus* dispersed out of Africa during the Middle Miocene. The data presented here along with reports in the literature suggest that colonization of North America via Europe may occur more frequently than colonization of Europe via North America (Szövényi et al., 2008), supporting

a possible Africa/South America–Europe-North America dispersal route. In the opposite direction, dispersal from the Palearctic to Australia probably occurred twice in *Entosthodon s.l.*, once in *Entosthodon muhlenbergii* which is disjunct between the two regions, with the the second dispersal into Australia being the species *Amphoritheca producta*. The biogeographic pattern is not unique to *Entosthodon s.l.*; for example, a number of species in the genus *Pohlia* exhibit disjunctions between parts of the Holarctic and Australasia (Shaw, 2006). Dispersal from Europe to Africa is reconstructed as happening only once, to the ancestor of *Entosthodon lepervanchei* and *Entosthodon claudineae*, during the Early Pliocene.

3.4.5. Climatic niche evolution

The climatic niche within the three lineages mirrors the biogeographic situation in that shifts occur frequently and are spread out across the tree. Parallel evolution of climatic niches occurs among all three lineages to varying degrees. In the Funariella-Physcomitrellopsis clade, Mediterranean and Tropical niches each evolved twice. In *Amphoritheca* temperate oceanic niches evolved twice. In *Entosthodon s.s.*, the Mediterranean climatic niche evolved at least three times, the temperate oceanic niche 5 times and the temperate steppe climatic niche evolved twice. In theory, species and clades in which climatic tolerances can evolve rapidly may diversify more rapidly by spreading into many different environments, thereby reducing competition and creating additional opportunities for speciation (Kozak and Wiens, 2010). Climatic-niche lability could also help buffer clades from extinction by helping species adapt when climate changes (Holt, 1990).

The appearance of Mediterranean climates within the last 10 Ma and the opening up of new areas of niche space are likely to have had an influence on

diversification of the group. Reconstructions of Mediterranean-climate ancestors in the Funariella-Physcomitrellopsis clade are congruent with the onset of hot dry summers and cold, wet winters in the Southern Hemisphere. The divergence of Mediterranean climate species in *Amphoritheca* at *ca*. 21.2 (14.9–27.1: 95 % HPD) Ma, however, predates the age of a Mediterranean climate in Europe. It is not uncommon for lineages to predate the age of their vegetation type (e.g. Verboom et al., 2009). Many angiosperms with Madrean-Tethyan disjunctions exhibit divergences that predate the age of Mediterranean climates (Wen and Ickert-Bond, 2009). Similarly, in *Entosthodon s.s.*, the reconstruction of a Mediterranean ancestor for the rhomboideus clade is not congruent with the climate at the time. The age of the two Mediterranean species, *E. bergianus* 12.8 (8.7–16.7: 95 % HPD) Ma and *E. limbatus* 4.5 Ma (2.3–7: 95 % HPD), in the attenuatus clade is more in line with the age of Mediterranean climates in the Southern Hemisphere.

Interestingly, a correlation may exist between dispersal, speciation and the evolution of a new climatic niche. Long distance dispersals, which are often followed by divergence and speciation, often coincide with a change in the climatic niche in *Entosthodon s.l.*. At what stage climatic niche change occurs, i.e. pre- or post-speciation is a topic for future research which could shed light on the influence of climatic niche lability on rates of diversification. Kozak and Wiens (2010), for example, showed that rapid species diversification is associated with accelerated climatic-niche evolution in plethodontid Salamanders.

In general, the rate of climatic-niche evolution may depend on the rate of evolution of physiological tolerances to environmental conditions such as temperature or drought (Kozak and Wiens, 2010). The attenuatus clade is almost entirely confined to tropical and temperate habitats, with a distribution that spans the entire world, save the Boreal and Polar Regions. Although the majority of species

in the clade originate from tropical latitudes, these species tend to occupy mid to high elevation habitats in the tropics which possess climates resembling temperate systems. This similarity of climate probably facilitated speciation between the two geographic zones.

It may be easier for annual species to shift climatic niche because they would only have to adapt to half a year's worth of climatic variation compared to perennial plants. Perhaps the biggest physiological hurdles would be adjusting the photoperiodical control of reproduction and temperature cues for germination. Hohe et al. (2002) recently demonstrated that short days promoted sporophyte development in *Physcomitrella*. Changes might be particularly difficult for shifts to a winter growing period i.e. Mediterranean climates, because environmental cues are likely to be completely reversed. Dietert (1980) found that the optimum temperature for germination of *Funaria hygrometrica* was 30ºC, but the optimum for the growth of the protonema was only 25ºC. The higher temperature requirement for germination is not unusual among plants because it insures a lower chance that an extreme frost event will kill young plants (Glime, 2003). In areas with a winter rainfall such a response would result in sure death as plants would emerge during a hot, dry summer period. These factors, in combination with the young age of Mediterranean climates, could possibly account for the lower diversity of Mediterranean clades because shifts between a winter and summer rainfall climatic niche would be more difficult and likely affect rates of speciation.

3.4.6. Conclusion

Evidence presented here supports a recent and rapid diversification of *Entosthodon s.l.* and the Funarioideae. This is paralleled by high rates of evolution of climatic niche space and high rates of long distance dispersal. Speciation may be happening mostly through allopatry after LDD and sometimes by ecological speciation

or a combination of the two, although this is only speculation.

Emergence of Mediterranean climates within the past 10 Ma may have triggered radiations within some clades. Evolution of a winter rainfall climatic niche, probably requiring a number of physiological modifications, may have affected these clades by reducing their ability to transition back into a summer rainfall niche. To better understand the rapid diversification of the Funarioideae, future work needs to determine whether a link exists between character lability and diversification rates. A better understanding of morphological evolution, in particular that of the sporophyte and whether this is linked to emergence of Mediterranean climates, will help to determine further potential correlates of diversification.

The rapid and often convergent change of character states has resulted in the presence of significant homoplasy within each of the lineages with respect to geography and climatic niche. Thus a note of caution is needed when interpreting the ancestral character state reconstructions in *Entosthodon s.l.* as these processes have undoubtedly had an effect on the probability of reconstructing the 'correct' character states along the tree. Including missing species and resolving problematic relationships in the subfamily may help to verify the results presented here.

4. Morphological convergence and correlated trait evolution in the Funarioideae sporophyte

4.1. Introduction

A fundamental challenge for evolutionary biologists is to understand the mechanisms whereby differences in traits across species evolved from a common ancestral state. The fossil record is replete with such evolutionary transformations, for example the evolution of insect wings from incipient pre-flight wings (Kukalova-Peck, 1978); yet for many taxa and character types good fossils are lacking (Cunningham et al., 1998; Huttunen et al., 2008). An alternative to fossil evidence is the reconstruction of ancestral states by mapping the character states of living organisms onto phylogenies. Phylogeny-based inference of ancestral states is an efficient and widely applicable means of investigating phenotypic evolution (Pagel, 1999a; Skinner and Lee, 2010) and is often the only source of important information on the timing and order of character change and on the number of times a character state has evolved independently (Coddington, 1988; Cunningham et al., 1998; Donoghue, 1989).

Repeated (convergent or parallel) evolution, the independent emergence of similar traits in separate evolutionary lineages, is of particular interest. It is often

taken as evidence of adaptation via natural selection, or of constraint on development that restricts the evolution of morphology (Gamble et al., 2012; Losos, 2011). Detecting cases of convergent evolution is central to understanding the adaptive significance of characters as these provide natural replicates that can illuminate the significance of particular features, as well as identify correlates of their evolution. Establishing the adaptive significance of a character, however, can be extremely difficult because similar features can evolve by differing mechanisms and species may respond to similar selection pressures by evolving non-convergent adaptations (Losos, 2011). Recent phylogenetic reconstructions have highlighted the prevalence of reductions in sporophytic characters across the mosses, and show that these reductions can converge to similar morphologies in even distantly related lineages (Bell and Hyvönen, 2010; Buck et al., 2000; During, 1979; Goffinet et al., 2011; Goffinet and Shaw, 2002; Hedderson and Longton, 1995; Hedderson et al., 1999; Hedenäs, 2000; Liu et al., 2012; Magombo, 2003; Pokorny et al., 2012; Renzaglia et al., 2007). Sporophytic reductions are generally thought to reflect a loss of function and therefore a loss of selection pressures maintaining complex dispersal-centric sporophyte architectures (Beike et al., 2014; Vitt, 1981). For example the loss of the peristome in the Orthotrichoideae may have occurred because the selective pressure to maintain a functional peristome was lost with the move into xerophytic environments. Vitt (1981) and Beike et al. (2014) posited that reductions in *Physcomitrella* were the result of the creation of a new ecological niche i.e. spores resting in mud and potential dispersal by birds.

The Funariaceae, a family of mosses well known for including numerous, variably reduced members, has received much recent attention (Beike et al., 2014; Liu et al., 2012; McDaniel et al., 2010). The family is characterized by a, relatively, uniform gametophyte morphology in contrast to that of the sporophyte

which displays significant architectural variability (see Figure 4.1). Within the family, the genus *Funaria* possesses the most complex sporophyte architecture, comprising a functional double peristome and exserted, zygomorphic capsules. In comparison, sporophytes in species of the Physcomitrium lineage (see Chapter 2) lack peristome teeth, and have simple, radially symmetric, capsules, which can be immersed among the perichaetial leaves or more often exserted above the gametophyte as in *Funaria*. The sporophytes of *Physcomitrella spp.* are the most reduced within the Physcomitrium lineage and the Funaricaeae, producing simple, immersed sporophytes lacking a dehiscent operculum. Species of *Entosthodon s.l.* produce a range of sporophyte architectures and the group includes species with complex sporophytes as well as species with variably reduced morphologies, including many intermediary forms. Because of its variability, the sporophyte has long served as a basis for the supraspecific classification of taxa within the Funariaceae. However, recent work has shown that numerous characters relating to the sporophyte, including several that have been deemed of taxonomic importance in the family, are homoplasious and that reduced sporophytes have evolved multiple times throughout the history of the Funariaceae (Beike et al., 2014; Liu et al., 2012; McDaniel et al., 2010, Chapter 2).

The primary function of the bryophyte sporophyte is the production and subsequent dispersal of sexually produced spores (Vitt, 1981; Grout, 1908). The components comprising the moss sporophyte are believed to serve different functions during dispersal. The seta elevates the capsule from the ground allowing spores to be taken up by air currents, placing a greater distance between parent and offspring. Besides the primary role of storage, the shape and orientation of the capsule aid dispersal of spores especially in vertical, epiphytic habitats (Huttunen et al., 2012; Vitt, 1981; Grout, 1908). The peristome, a feature which is believed to have evolved independently at least twice within the mosses (Bell

Hyvönen, 2008), generally relies on hygroscopic movement of its teeth to control when spores are released into the environment.

Variations on these components are organized into distinct and recurring life history syndromes which appear to be associated with particular sets of environmental conditions (Hedderson and Longton, 1995). In mosses in particular, the loss of dispersal enhancing features, coupled with an increase of spore size and annualism, is associated with environments experiencing moderate levels of stress, e.g. xerophytic habitats, and where habitats are transient, surviving no more than a few years e.g. soil in rock crevices or grasslands (During, 1979; Hedderson and Longton, 1995; Vitt, 1981). In these situations the need for greater allocation of energy into reproduction and the fact that favourable habitats tend to occur within the same landscape is thought to be responsible for the loss of dispersal enhancing features (During, 1979; Longton and Hedderson, 2012). The potential functional significance of sporophytic reductions has thus been well established, however, little is known about how these traits evolve. In particular, the order of evolution underlying shifts between complex sporophytes and those that are completely reduced has so far never been investigated.

The Funariaceae provide an interesting stage on which to test hypotheses regarding the order of evolution in sporophyte morphology. If indeed selection, or the lack thereof, is driving sporophytic reductions then we may posit that an absence of selection for dispersal enhancing features should result in the gradual loss of those complex features in favour of simpler and cheaper versions. Further, the order by which simplification occurs could be by two different mechanisms, either i) loss of complex features is random and hence there is no ordered sequence of change, or ii) loss of complex features occurs in a specific sequence. If change is ordered this would suggest a functional association and provide some of the first evidence that the components of the sporophyte work together forming

a functional unit.

To better understand the convergent evolution of sporophyte morphology in the Funarioideae the aims of this chapter are to: i) reconstruct ancestral character states of the Funarioideae sporophyte and the degree of homoplasy exhibited by these; ii) test whether changes in sporophyte character states are correlated; iii) determine the order of evolution and gradual reduction in the Funarioideae sporophyte, and; iv) speculate on the possible adaptive significance of these changes in the context of their life history strategy.

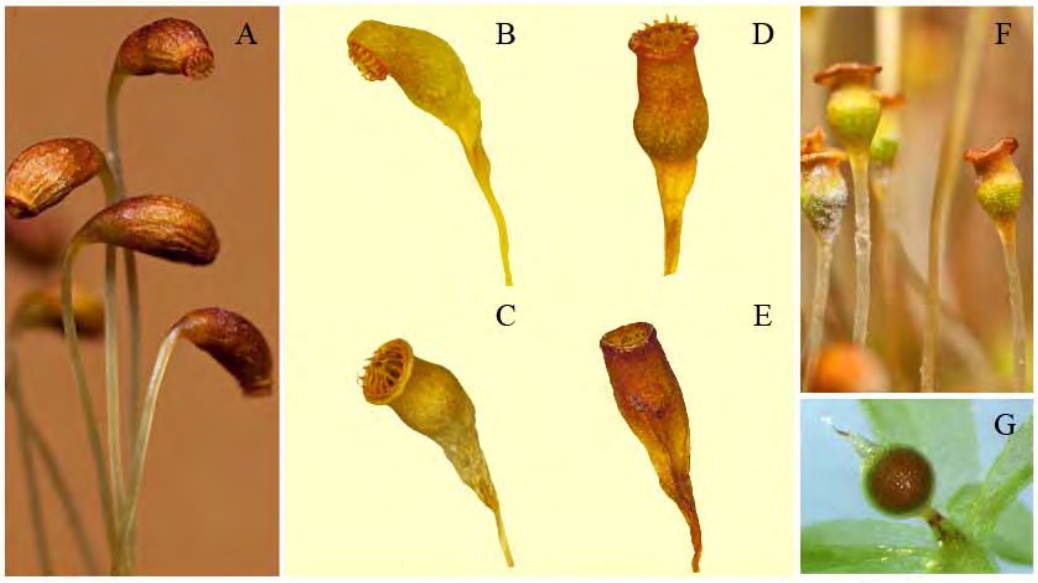

Figure 4.1: The diversity of sporophyte architectures in the Funarioideae. *Funaria hygrometrica* Hedw. (A), showing the most complex sporophytes in the family; *Entosthodon s.l.* spp. (B-E). This illustrates the range of intermediate capsule architectures observed in the subfamily; *Physcomitrium pyriforme* (Hedw.) Hampe (F), showing reduced sporophytes; *Physcomitrella patens* (Hedw.) Bruch & Schimp. (G), a species displaying completely reduced sporophytes, with cleistocarpic capsules that lack functional setae. Images: A - (Image: http://ohiomosslichen.org/bryology-plants/ - accessed 6/7/2015); F - (http://ohiomosslichen.org/?attachment_id=5054 – accessed 6/7/2015); G - (Image: http://www.plant-biotech.net/bryotechnology_gallery/#5 - accessed 6/7/2015).

4.2. Materials and Methods

4.2.1. Scoring of morphological characters

The states of three key characters: i) the presence or absence of a peristome, ii) capsule symmetry and iii) exserted vs. immersed sporophytes, summarizing much of the morphological diversity in the sporophytes of the Funarioideae were coded as binary states (see Appendix A, Table A.3). For the peristome, species with a rudimentary (non functional) peristome were scored as peristome absent. Capsule symmetry was scored either as radially symmetric or zygomorphic. Species that are only weakly zygomorphic, for example those with a slight bend in the necks of the capsules, were treated as symmetrical. Though unrelated to the sporophyte, the presence of a fourth taxonomically important trait, limbate or bordered leaves, was binary coded for each species.

4.2.2. Reconstruction of ancestral states

Maximum Likelihood (ML) and Bayesian Inference (BI) approaches were used to reconstruct ancestral character states for each of the four characters mentioned above. I applied both methods since each varies in the assumptions made and potentially in the results they provide (Cunningham et al., 1998). BI was used to reconstruct ancestral states of the deeper nodes in the tree while ML reconstructions were performed for all nodes on the tree. Nodes for BI analyses were picked based on clade size and position in the phylogeny in order to fully capture evolutionary transformations across the tree. ML reconstructions were conducted using Mesquite v2.75 (Maddison, W. P., 2011) on the BI majority-rule consensus tree from Chapter 2, with tips pruned so that each species is represented only once in the phylogeny. In each case the most likely of the two models implemented in Mesquite, the Markov k-state (MK1) model (Lewis, 2001) or the asymmetric 2

parameter model (Asymm. 2 param.), was chosen to reconstruct ancestral states. By using a Bayesian approach to character evolution, uncertainties in topological relationships and evolutionary distances can be accommodated among nodes and species when inferring ancestral states (Pagel and Meade, 2006). The BI approach applied here used the 'Multistate' option in BayesTraits v1.0 (Pagel and Meade, 2006) on a set of 4500 trees generated by BI. BayesTraits has the advantage of being able to test numerous models by employing a reversible jump (RJ) Markov chain Monte Carlo (MCMC) which searches the posterior distribution of different models of evolution as well as the posterior distributions of the parameters of these models. Ancestral states were reconstructed for ten key nodes using a RJ hyperprior (RJHP), with an exponential prior seeded from a uniform distribution on the interval 0-10. A hyperprior is simply a distribution, usually uniform, from which values are drawn to seed the values of the exponential gamma priors. Hyperpriors provide an elegant way of reducing some of the uncertainty and arbitrariness associated with choosing priors in MCMC analyses (Pagel and Meade, 2006). Analyses converged after 10 million generations and a burnin of 10 perecent was used. The AutoTune option was used to find an optimal RateDev parameter. The likelihood of alternative character states was tested at each node using the 'fossil' command to fix nodes in alternate states and by calculating a BayesFactor (BF) using the harmonic means, derived from the posterior probability of likelihood values of the alternative character states. Interpretation of BF followed Pagel et al. (2004), i.e. support for any particular state was considered positive when BF = 2log [harmonic mean (best model)] $_{l}$og [harmonic mean (alternative model)] was >2, strong evidence for values >5, and very strong evidence for values >10.

4.2.3. Correlated trait evolution

An additional character, mean length of seta < or > 1 cm was scored (see Appendix A, Table A.3) and tested for correlated evolution with capsule symmetry and with the peristome. This character was thought to offer a more accurate signal of any potential correlated evolution between characters because it varies more within the subfamily. Immersed sporophytes are largely confined to the Physcomitrium lineage, all species of which lack peristome teeth and have symmetrical capsules. A BI approach, as implemented in BayesTraits, was used to determine whether characters evolve independently of each other. The method compares the fit of two evolutionary models for two discrete characters, i.e. a model of correlated evolution (dependent evolution; D) employing up to eight rate parameters for dual character state transitions and an independent model of character evolution (I) with up to four rate parameters. A RJHP MCMC sampled trees and model parameters in proportion to their posterior probabilities under the D and I models. Rate priors were sampled, as above, using the RJHP seeded from a uniform distribution between 0 and 10. As with the previous analyses the AutoTune option was used to find an optimal RateDev parameter. Each RJHP MCMC was run three times for 10 million generations and for all combinations of sporophyte morphological characters. Bayes Factors were used to estimate support for the two models. Support for correlated evolution was also evaluated by comparing the ratio of prior and posterior odds for visits in I and D models during the chains (Pagel and Meade, 2006). Support for either model was estimated by use of BF. This approach is based on a property of the RJHP MCMC that in the chain in which all eight dual character-state transitions can occur freely, the number of visits to the dependent or independent model is proportional to the posterior probability of the model (Pagel and Meade, 2006).

To determine the order of character evolution in the Funarioideae sporophyte,

three different methods were used based on a similar study by Huttunen et al. (2012). First, ancestral state reconstructions were compared for the different sporophytic character states. Second, rate coefficients were sampled from the best of three RJHP analyses with the dependent model of evolution. The rate coefficients of the D model describe the 8 possible transitions between the 4 different character combinations of the two binary traits. The rates of interest were those that described transitions where the first morphological character remains unchanged while the second character changes (qX), and where the second morphological character remains unchanged while the first character changes (qY). A difference in the posterior distribution of rate coefficients (qX and qY) was tested for each character combination using the nonparametric Mann-Whitney t-test. Third, evolutionary significance of difference in rate coefficients was confirmed by running an analysis with the dependent model of evolution and with a restricted dependent model where qX and qY were set to equal using the same settings for the analyses as above. The fit of these models was compared with BF's based on harmonic means of the posterior probability of likelihoods.

4.3. Results

4.3.1. Reconstruction of ancestral states

The Asymm. 2 param. model of character change was used for all ML reconstructions. For the peristome and symmetry reconstructions the model was implemented for consistency as differences in likelihood from the Mk1 model were negligible.

The results of the ancestral state reconstructions are presented in Figures 4.2 to 4.5. The BI and ML analyses (Figure 4.2) support the presence of a peristome in the most recent common ancestor (MRCA) of the Funarioideae (BF=positive

evidence). The pleisiomorphic condition was lost early on in the ancestor of the Funariella-Physcomitrellopsis/Amphoritheca/Physcomitrium/Entosthodon lineages, and later regained in the MRCA of *Amphoritheca*, *Entosthodon s.s.* and the Physcomitrium lineage. Peristome teeth have been lost and regained no fewer than 6 and 6 times respectively (or regained up to 10 times assuming all losses in the crown polytomy are independent). The BI and ML reconstructions are congruent across the tree with minimal differences in support for ancestral states. A minimum of positive support from BFs is present for every node except for the MRCA of the *Entosthodon s.l.* and Physcomitrium lineages, however, BI and ML approaches both give almost equivalent probabilities to the ancestral state at this node.

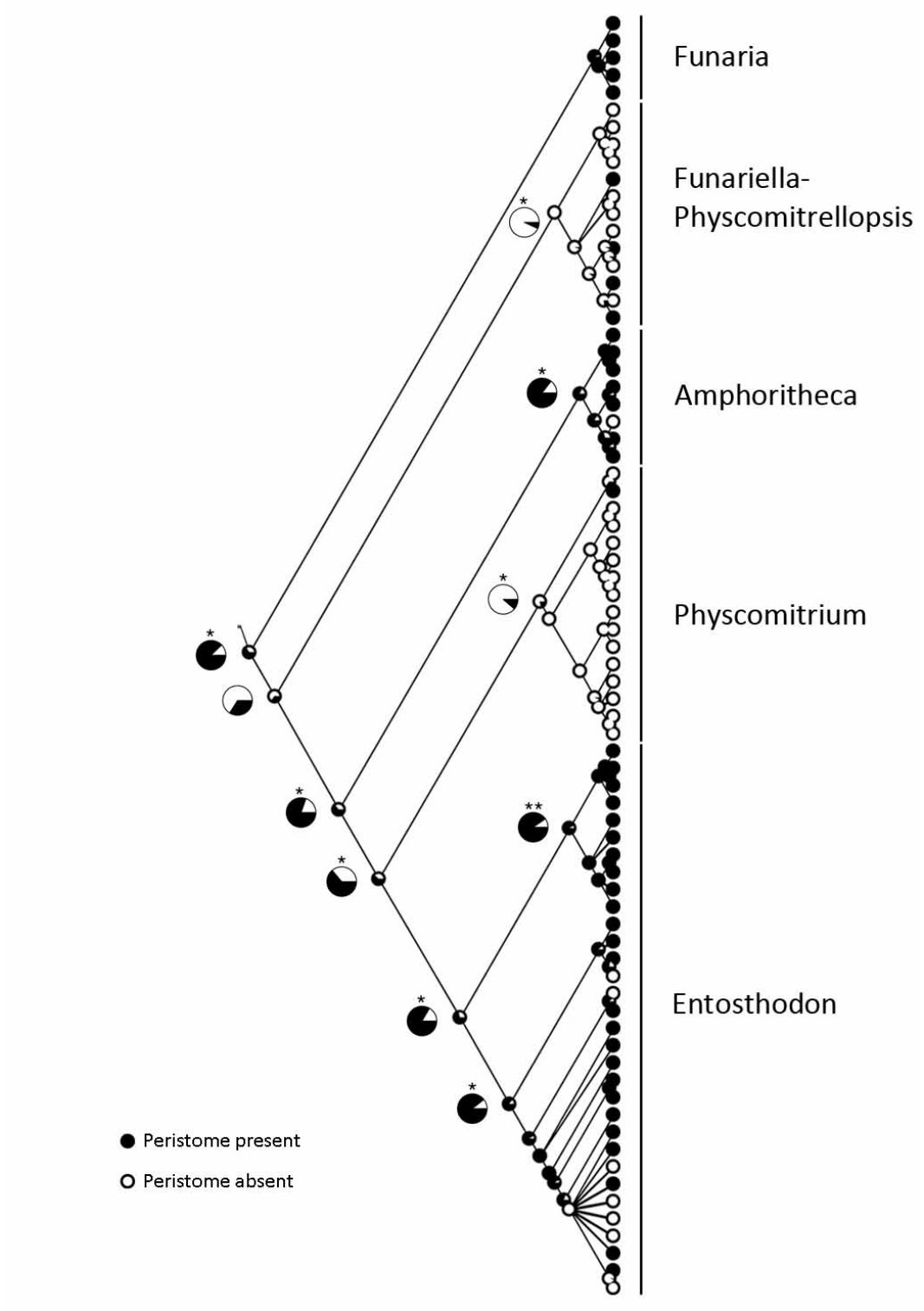

Figure 4.2: Ancestral character state reconstructions using BI and ML methods for the peristome. Small internal circles represent likelihoods of a particular character state under the ML reconstruction and large external circles are posterior probabilities from the BI reconstructions. The stars above the BI circles are levels of support given by BayesFactors (* positive, **strong, ***very strong).

According to the ML reconstructions radially symmetric capsules (Figure 4.3) were lost and regained 3 and 9 times respectively. The BI reconstruction strongly supports an ancestor with a zygomorphic capsule compared to only marginal support for a radially symmetric ancestor in the ML analysis. Assuming that the BI root state is more likely, the number of independent gains and losses would be 8 and 4 respectively. Overall, reconstructions under BI and ML are congruent, differing only at the root, as mentioned above, and at node x; a sub-clade of *Entosthodon s.s.*, where support is not convincing in either of the analyses.

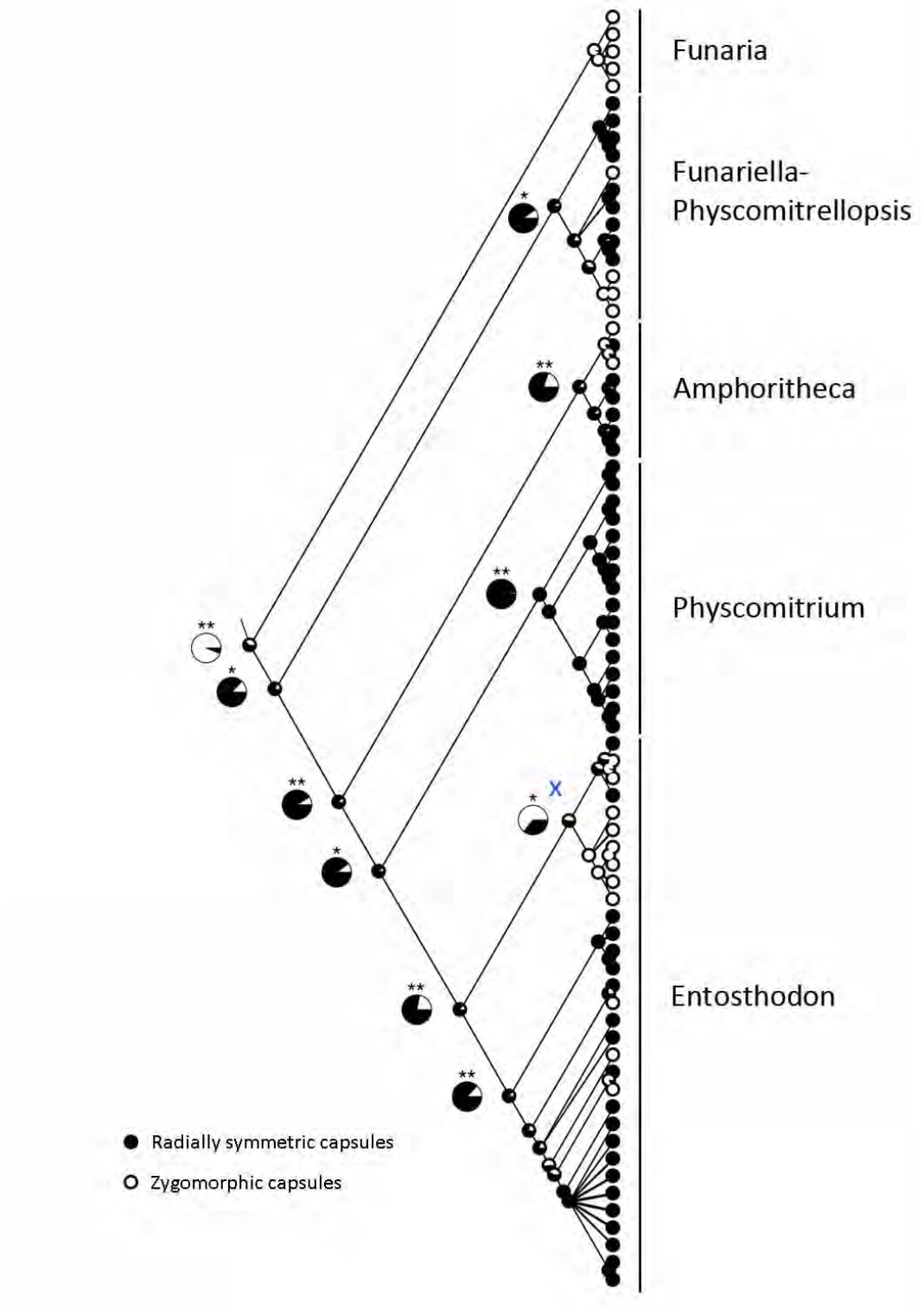

Figure 4.3: Ancestral character state reconstructions using BI and ML methods for capsule symmetry. Small internal circles represent likelihoods of a particular character state under the ML reconstruction and large external circles are posterior probabilities from the BI reconstructions. The stars above the BI circles are levels of support given by BayesFactors (* positive, **strong, ***very strong). The blue 'X' denotes a node where BI and ML reconstructions are not congruent.

Immersed sporophytes have evolved at least four times and been lost twice in the subfamily (Figure 4.4). BI and ML inferences obtained congruent results. All gains in immersed sporophytes take place close to the tips and as a result BI reconstructions do not recover any deep ancestors with immersed sporophytes, Bayes Factors thus offer little support in this instance.

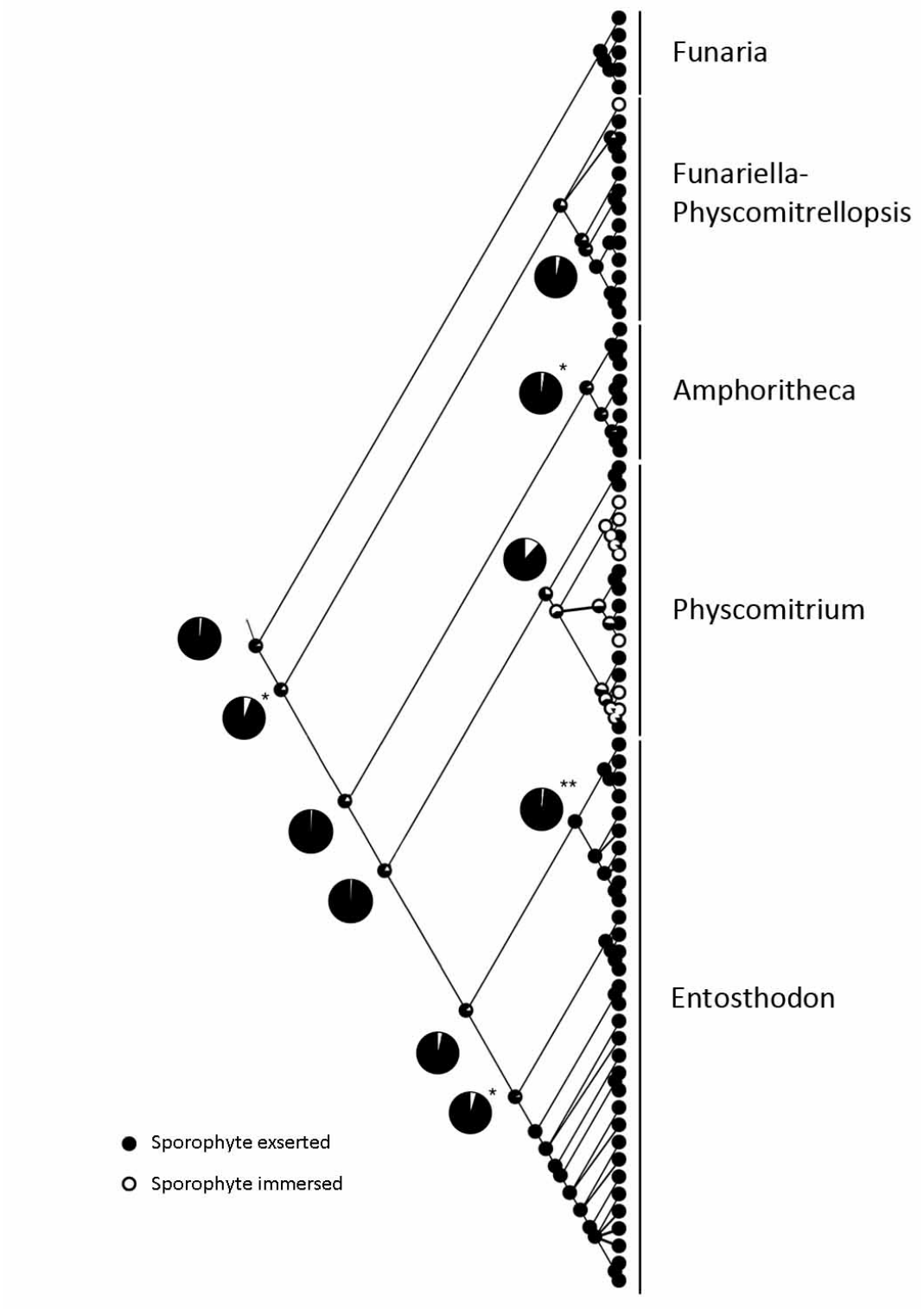

Figure 4.4: Ancestral character state reconstructions using BI and ML methods for immersed & exserted sporophytes. Small internal circles represent likelihoods of a particular character state under the ML reconstruction and large external circles are posterior probabilities from the BI reconstructions. The stars above the BI circles are levels of support given by BayesFactors (* positive, **strong, ***very strong).

Limbate leaves have evolved 9 times along the Funarioideae tree (Figure 4.5) and have been lost twice. The MRCA of the Funarioideae is reconstructed with elimbate leaves although with no support from BFs. Overall BFs confer strong support for elimbate ancestors over much of the tree. BI and ML reconstructions are highly congruent, placing almost equivalent probabilities on ancestral states.

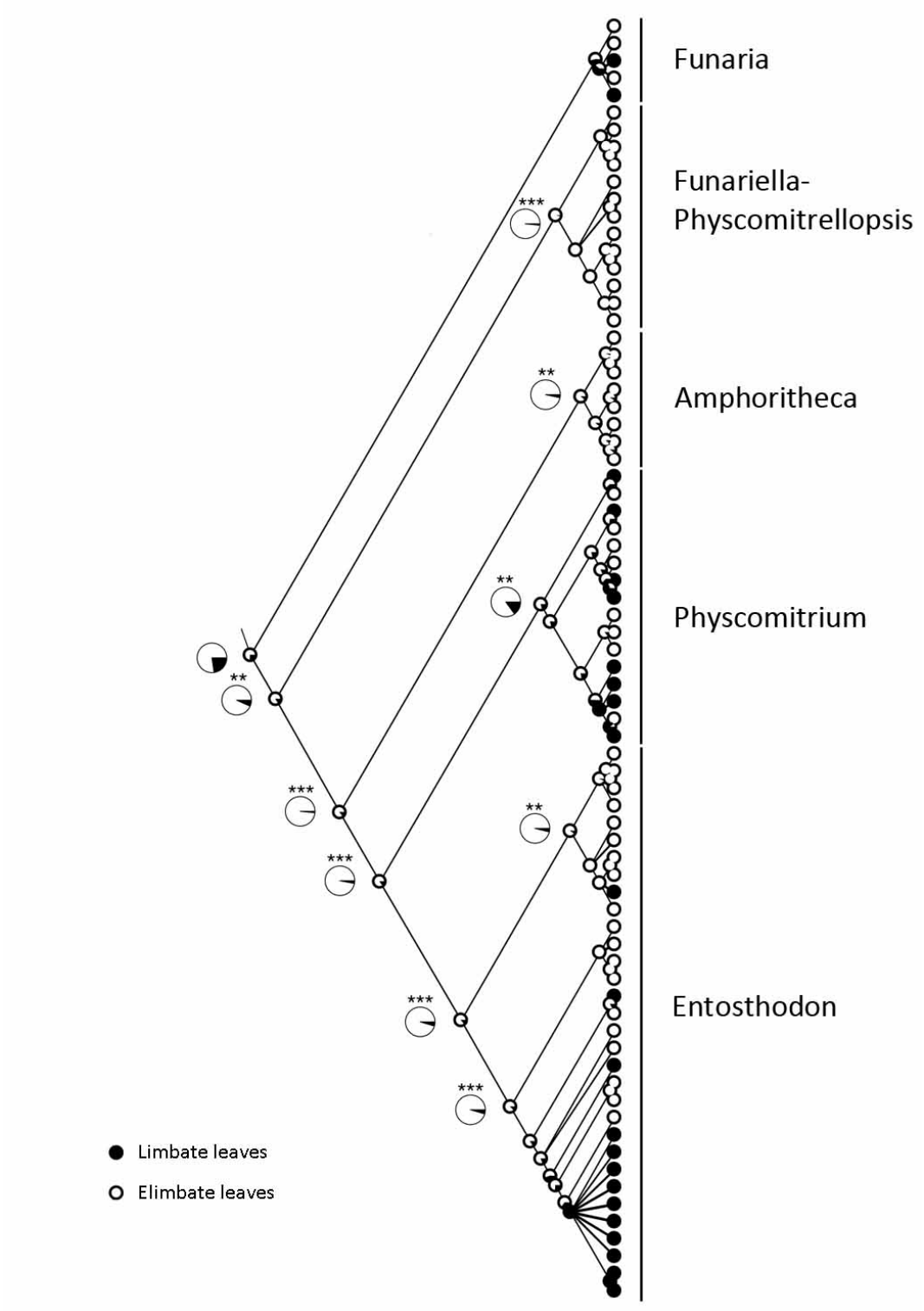

Figure 4.5: Ancestral character state reconstructions using BI and ML methods for limbate leaves. Small internal circles represent likelihoods of a particular character state under the ML reconstruction and large external circles are posterior probabilities from the BI reconstructions. The stars above the BI circles are levels of support given by BayesFactors (* positive, **strong, ***very strong).

4.3.2. Correlated evolution of characters

Harmonic means of log-likelihood scores sampled by the RJHP MCMC chains were significantly higher for D models than for I models (Table 4.1) in two out of three character combinations. Strong support exists from BFs for the dependent (correlated) evolution between capsule symmetry and the peristome and there is very strong support for dependent evolution between the length of the seta and the peristome. However, there is no evidence for correlated evolution of seta length and capsule symmetry. Chains did not visit I models at all for the character combinations 1 & 3 (Table 4.1), with strong BF support, providing the highest possible support for correlated evolution between these characters. For the combination of symmetry and seta length, I models were visited by the RJHP MCMC more frequently than expected resulting in a negative BF and instead providing support for the independent model.

Table 4.1: Results from tests for correlated evolution between three morphological characters of the Funarioideae sporophyte. Test results based on i) comparisons of harmonic means of likelihoods (lnL) from reversible-jump Markov Chain Monte Carlo (RJ MCMC) runs with an independent (I) and a dependent (D) model of character evolution; and ii) average numbers of visits to I models during RJ MCMC runs for 3 runs. The mean of harmonic means (mean lnL), standard deviations (st.dev. lnL), and maximum harmonic mean of likelihood (max lnL) of three I and D runs are given. Bayes Factor (BF) values were calculated using the maximum harmonic mean of likelihood from the best I and D run, i.e. the run yielding the highest likelihood after 10 000 000 iterations (I max lnL and D max lnL in the table). For ii) chains were run three times, and for the best run the number of visits to I models was compared with the prior odds. BFs >5 based on prior and posterior odds give support for unexpectedly high number of visits to D models, strongly supporting the evolutionary model assuming correlated evolution between morphological characters. When visits to I models are absent, a non-applicable (NA) BF is the result of a 0 in the divisor. BF >5 are considered strong evidence for correlated evolution and are in bold.

Characters	D mean lnL	D st.dev. lnL	D max lnL	I mean lnL	I st.dev. lnL	I max lnL	BF	Number of I visits	posterior odds	posterior/prior odds	BF
1) Symmetry + Peristome	-74.25	0.40	-73.93	-78.54	0.21	-78.40	**8.93**	**0**	NA	NA	NA
2) Symmetry + Seta	-77.96	0.30	-77.77	-77.93	0.16	-77.83	0.13	**163**	55.21	0.13	-4.03
3) Seta + Peristome	-81.19	0.60	-80.69	-87.44	0.81	-86.81	**12.24**	**0**	NA	NA	NA

Rate coefficients for character state change (Table 4.2) indicate that the order of sporophyte reduction in the Funarioideae started with a shortening in the length of the seta, followed by the capsule becoming radially symmetric and finally loss of the peristome layers. In each case, the rate coefficient qX (first character constant, second character changes from ancestral to derived state) was significantly larger than qY (second character constant, first character changes from ancestral to derived state). Only in character combination 3 (peristome + seta; Table 1) was the fit of the evolutionary model, where rates were allowed to vary freely (full 8 parameter model), a significantly better fit to the data compared to the model where rates were restricted to be equal (qX=qY, i.e. 7 rate parameter model).

Table 4.2: Comparisons between rates of dual character state change between morphological characters of the Funarioideae sporophyte. The rate coefficient for character change where the first character remains unchanged while the second character changes ([0,0]–[0,1]) is qX, and qY is the rate of the change where the second morphological character remains unchanged while the first character changes ([0,0]–[1,0]). Difference in rates was tested by running an MCMC chain applying the model of dependent evolution for morphological and habitat character state change (D; 8 parameters) and with the restricted model where qX and qY were forced to be the same (R; 7 parameters). Bayes Factors (BF) were used to estimate whether the difference in likelihoods for R and D models was statistically significant. For both R and D models, MCMC runs were repeated three times and their means are shown in the table; D runs (mean lnL D) and R runs (mean lnL R). BF's were calculated based on the best run, i.e. with the highest likelihood (max lnL D and max lnL R). BF's > 5 were regarded as conferring strong support. Rate coefficients were also sampled during MCMC chains with a D model and used for testing the difference between qX and qY. Means and standard deviations for the rate parameters (columns qX and qY) from the run yielding the best likelihood are given and significance of differences between the rates is tested.

Characters	mean lnL D	max lnL D	mean lnL R	max lnL R	BF	qX	qY	p	Mann-Whitney U
1) Peristome + Symmetry	-74.38	-74.03	-74.09	-73.65	-0.76	**1.48**	0.85	**0**	21626883
stdev	0.52		0.45			1.07	0.61		
2) Symmetry + Seta	-78.63	-77.99	-78.02	-77.57	-0.84	**2.38**	1.92	**0**	48199298
stdev	0.57		0.59			1.70	1.34		
3) Peristome + Seta	-80.52	-79.81	-82.27	-81.72	**3.82**	**4.69**	1.20	**0**	5591293
stdev	0.65		0.48			2.98	0.85		

4.4. Discussion

Sporophyte architecture in the Funarioideae is remarkably labile and is characterized by multiple, independent shifts between a more complex pleisiomorphic state and functionally reduced state. The relationship between character state shifts between i) the peristome and seta and ii) the peristome and capsule symmetry, are correlated in such a way that certain combinations of changes are more likely than others. It therefore seems likely that the evolution of a completely reduced sporophyte occurred via an ordered sequence of change.

4.4.1. Ancestral character states in the Funarioideae and convergent evolution of sporophyte morphology

Peristomate, zygomorphic, exserted sporophytes are reconstructed as the ancestral condition in the MRCA of the Funarioideae. Among the five major lineages, *Funaria* is the only lineage to retain fully all ancestral features of the sporophyte; although not included here *F. polaris* Bryhn is only very weakly zygomorphic. This ancestral type sporophyte was lost and re-acquired numerous times among *Entosthodon s.l.* but was never re-acquired in the Physcomitrium lineage, the lineage with multiple independent reductions to a completely reduced sporophyte i.e. a radially symmetric, immersed sporophyte lacking a peristome. The reconstruction of character states in the MRCA of the Funarioideae could be affected by additional sampling. In particular, including members of the Pyramiduloideae would likely have an effect on reconstructions of capsule symmetry in the MRCA of the Funarioideae, because zygomorphic capsules are not common outside of *Funaria*, but this would probably not significantly alter any of the other character state reconstructions.

The loss and reacquisition of complex characters has received much atten-

tion in the literature, particularly in tests of Dollo's Law, which states that once a complex structure is lost it is unlikely to be reacquired (Gould, 2002, 1977), with many studies offering evidence to the contrary (Collin and Cipriani, 2003; Collin and Miglietta, 2008; Domes et al., 2007; Galis et al., 2010; Kohlsdorf and Wagner, 2006; Lynch and Wagner, 2010; Wiens et al., 2007; Zander, 2006). Novel evo-devo and genomic applications are now showing that developmental pathways can be maintained for tens of millions of years, and are slowly eroding the idea that the genes underlying unexpressed characters have been lost to random mutation (Collin and Miglietta, 2008; Marshall et al., 1994). When considering the frequency of losses and gains of pleisiomorphic character states and the strong similarity of these states between even distant lineages it is possible that the relevant genes responsible for the pleisiomorphic architecture were never completely lost. Gene silencing followed by reactivation could explain the re-evolution of pleisiomorphic states (Collin and Cipriani, 2003; Marshall et al., 1994). Estimates of mutation rates from structural genes show that there is a significantly high probability of reactivating silenced genes over time scales of < 6 Ma (Marshall et al., 1994) before full or partial degradation to non-functionality. Similarly, this could be relevant to apomorphic states. If genes are being silenced and reactivated, then only isolated losses of complex states may represent cases of true convergent evolution within the subfamily. For example, the current reconstructions provide evidence for four independent shifts to immersed sporophytes. If, however, developmental pathways are maintained then it is possible that this instead only occurred twice. Only by identifying the presence or absence of the relevant developmental pathways will we be able to determine whether genes are evolving de novo or whether dormant genes are being re-expressed.

4.4.2. Evolution of sporophytic characters, its potential adaptive significance and prospects for future research

Examples of correlated evolution between different morphological traits are abundant throughout the literature (Buzatto et al., 2014; Derryberry et al., 2012; Higginson et al., 2012; Sun et al., 2014; Tonnabel et al., 2014; Vamosi et al., 2003) and are generally interpreted as evidence of a functional link, with most studies suggesting *a priori* that natural selection is responsible for driving evolutionary change.

Evolution between both the peristome and capsule symmetry and the peristome and the length of the seta (immersed/exserted sporophytes) is correlated, implying that a functional association between these characters has influenced the evolution of sporophyte architecture in the Funarioideae. The detection of correlated evolution provides some of the first evidence that the components comprising the moss sporophyte work together as a single functional unit and that change in one character can drive changes in others. Analyses of correlated evolution strongly support models of both directional and dependent morphological change, supporting an ordered sequence of morphological evolution in the sporophyte. Morphological change towards a reduced state probably started with the shortening of the seta, followed by a shift to a radially symmetrical capsule, and finally the disappearance of the peristome. Current knowledge supports the view that the evolution of sporophytic architecture is tightly linked to the environmental conditions and to the particular life strategy of the plants (During, 1979; Grout, 1908; Hedderson and Longton, 1995; Vitt, 1981). From an evolutionary perspective, the shortening of the seta may have rendered any other dispersal enhancing features of limited value, because spore dispersal would essentially be restricted to the vicinity of the gametophyte. This would likely lead to the loss

of other specialized features i.e. zygomorphic capsules and peristomes, in favour of producing a cheaper, simplified capsule, because of a potential gain in fitness from increased reproductive allocation.

The evolution and adaptation of the moss sporophyte remains a crucial yet little studied area of research. Grout (1908), among others (During, 1979; Hedderson and Longton, 1995; Longton, 1988; Vitt, 1981), based on numerous correlates of moss sporophyte morphology with specific habitat preferences, postulated that the morphology of the sporophyte is closely linked to the environmental conditions experienced by the plants. The presence of life history syndromes in mosses was suggested by During (1979, 1992) and Longton and Schuster (1983). Work on the topic has accumulated significant evidence supporting the presence of these syndromes (Hedderson and Longton, 1995; Hedenäs, 2001; Longton, 1988) and that these are independent of phylogenetic inertia (Crawford et al., 2009). Dispersal related traits, in particular, have been tightly linked to the evolution of sexual system in mosses (Crawford et al., 2009) and thus form an integral part of their life history.

Vitt (1981) further postulated that, among others, the Funariales exhibit features that are characteristic of plants inhabiting unpredictable habitats, for example: shortened life-cycles; cleistocarpous, gymnostomous capsules that are often ovate and immersed; shortened seta; bulbiform gametophytes; and increased spore size. Shortened life-cycles are presumably an adaptation to the unpredictable nature of the substrate and habitat itself. Shortening of the seta and loss of the peristome are both correlated with xerophytism (Hedderson and Longton, 1995; Vitt, 1981) and shortened life cycles are also commonly observed in xerophytic groups. Thus moves towards production of a simplified sporophyte are probably linked to a combination of the shortening of the life-cycle and predictability of the habitat (During, 1979; Hedderson and Longton, 1995).

Although not reconstructed here, members of the Funarioideae, notably *Physcomitrella*, produce a further simplified, more economical, immersed sporophyte. For example, the capsules of *P. patens* are thinner walled, lack a dehiscent operculum and are spherical in shape. A spherical capsule is the most economical capsule to produce as it offers the highest volume for surface area (isoperimetric theorem) allowing for the maximum reproductive allocation into spores. The greater allocation of resources into reproductive effort is thought to be an important feature in the life strategy of annual plants (During, 1979; Hedderson and Longton, 1995; Longton and Schuster, 1983).

Within the Funarioideae, reduced sporophytic features are particularly apparent within the *Physcomitrium* lineage. Species of this lineage are present in all but extremely cold climates and are common in habitats that are ephemeral such as flood plains and exposed river banks, where the arrival of water is often unpredictable between years and the substrate may be temporarily submerged. The loss of features enhancing dispersal in this group is particularly evident, along with the absence of any reversals to the pleisiomorphic state. The loss of dispersal enhancing features could be a result of two possibilities: i) favourable habitat is typically close by (Hedderson and Longton, 1995) and space is not limited or ii) dispersal is being achieved by other means, for example by birds or moving water. In comparison the species of *Funaria* are often found in more xeric conditions. Substrate type is also widely variable, from burnt logs to soils with significant lime or salt content to volcanic cinders and even lemming burrows, as in *F. arctica* Berggr. Kindb. (Hofmann, 1997). The spores of species of *Funaria* are significantly smaller than those of other genera in the subfamily and small spores are known to be better dispersed by wind (Miles and Longton, 1990). Given this fact, in combination with the complex sporophyte present in *Funaria*, it would not be unreasonable to assume that there is significant selection pressure

for character states promoting long distance dispersal.

If indeed changes in the morphology of the Funarioideae sporophyte are attributable to changes in habitat of the plants then perhaps the differences of habitat between *Funaria*, the lineage to fully retain the ancestral sporophyte, and the Physcomitrium lineage, which displays the most frequent moves to a reduced sporophyte and no gains of the ancestral morphology, can bring to light the adaptive significance of the pleisiomorphic vs. apomorphic condition. Using phylogeny-based comparative methods Huttunen et al. (2012) assessed the adaptive nature of sporophytic specializations in two families of mosses, the Neckeraceae and Lembophyllaceae, both of which show parallel shifts to a specialized morphology and to exposed epiphytic or epilithic habitats. The authors were able to show that some specializations, namely the length of the seta and two endostomal characters, had co-evolved with the shift to a new habitat. The authors were further able to show that the character change appeared after the shift to a new habitat supporting a possible adaptive significance. The next step for the Funarioideae is to understand why certain morphologies have re-evolved multiple times and a similar study could help provide support for a link between morphological evolution and shifts into different habitats. At the moment, detailed information on habitat for many species in the Funarioideae is lacking, limiting further investigation at this point.

4.4.3. The evolution of limbate leaf margins

Limbate margins are present in many families and have almost certainly evolved numerous times throughout the mosses, yet there is little speculation in the literature (Glime, 2007) concerning their potential role. Limbate margins are an important taxonomic character in the Funarioideae and an understanding of their evolution in the group is important when considering taxonomic decisions. If

limbate margins were subject merely to neutral evolution in the Funarioideae we might have expected gains to approximate losses, however, limbate margins are lost only twice and have been gained nine times, strongly suggesting a selective advantage for their presence. Mosses lack roots and specialized conducting tissues for the uptake of water, and are thus thought to have evolved numerous leaf traits associated with the acquisition and retention of water; elongated marginal cells may confer some advantage in this area (Glime, 2007; Schofield, 1981). The shape and position of limbidial cells suggests that they may have a function in regulating rigidity in leaves, either by keeping them flat and spreading under conditions when leaves that lack limbidia may already start to contort, or to the contrary they may aid coiling of the leaf which would aid in conservation of water by reducing the boundary layer around the leaves. Alternatively, their elongated shape, which means fewer cell wall boundaries to traverse, might aid in dispersing water more rapidly around the leaf (Glime, 2007).

4.4.4. Conclusion

Ancestral reconstructions support the parallel evolution of reduced sporophytes as well as re-evolution of complex sporophyte morphologies in the Funarioideae. However, the morphological similarity of a number of reduced forms points to potential ”underlying” homology of the structures and future work involving developmental pathways could help to resolve if this is in fact true. The correlated and ordered morphological evolution of the sporophyte provides some of the first evidence supporting the functional relationship between components of the moss sporophyte. Future work should now aim to establish potential drivers of sporophyte evolution in the Funarioideae by searching for further correlates of character change. In particular, the relationship of morphological change with

shifts into different habitats and whether these are the result of similar selective pressures should be the focus of future work. In addition, these should be combined with other methods, for example direct measurements of selection or investigations of the functional correlates of trait evolution to test hypotheses of adaptation. Finally, determining whether the appearance of certain character states is linked with rates of diversification will further help establish the importance of sporophyte architecture in the evolution of the mosses.

5. A Revision of the genus *Entosthodon* Schwägr (Bryopsida, Funariaceae) *sensu lato* in sub–Saharan Africa

5.1. Introduction

Here I present a taxonomic treatment of the African species previously treated under *Entosthodon*, including the monotypic genus *Physcomitrellopsis*. Twenty-six species are recognized for Africa under five different genera: *Amphoritheca* (3 species) *Entosthodon s.s.* (12 species), *Fifeobryum* (1 species), *Funariella* (9 species) and *Physcomitrellopsis* (1 species).

A key to the 26 African species of *Entosthodon s.l.* is provided. Given the absence of diagnostic synapomorphies for most of the genera (see Chapter 4), no attempt is made to provide a genus-level key. However, each genus is described in detail, and characters that can be used to determine generic identity are discussed. For each species, I provide a detailed description, photographic illustrations of key features, a discussion of diagnostic characters and, where applicable, differences from similar species. The known African distribution of each species is mapped.

5.2. Materials and Methods

About 1300 herbarium specimens were examined for the current study, from the following herbaria: BM, BOL, E, EGR, H, HBG, HUH, MO, MQU, NY, PRE, S, WU, Z. The study area includes the sub-Saharan countries and adjacent islands treated by O'Shea (2006) in his checklist of mosses for the region. I have further restricted this scope by only considering the strictly sub-Saharan flora and not those species whose southern most distribution lies within the Sahara. Extra-African species were examined if they were believed to be synonymous or putative relatives of the African species. Information on habitat and distribution were taken from herbarium labels, the literature and from personal knowledge.

Specimens were measured and observed under a Wilde stereo microscope when moist and under a Nikon compound microscope while immersed in water or Hoyers solution under coverslips. Macrophotography of plants was done while dry for two reasons: first, macro-features such as habit and capsule shape of plants are best examined when dry and don't require rewetting to aid in identification and second, photography of wet plants is extremely difficult because of constant movement caused by the drying of the plants and this is made even harder in groups like the *Funariaceae* that are thin walled and thus have a tendency to lose water at an even faster rate. Photography was performed using a Nikon Eclipse 50i compound microscope for plant material mounted on slides and a Nikon SMZ1500 stereo microscope for photographs of capsules and habits. Both microscopes used a Nikon DS Camera Control Unit DS-U2 and DS-5M Camera and the Nikon NIS elements digital 3D imaging software which automatically photographed and stacked images. Post-processing of images and creation of plates was done using Adobe Photoshop CS5.1 (Adobe Systems Inc.).

Measurements always represent the complete observed morphological varia-

tion of the species. Leaf cross-sections were always made in the middle portion of the leaf. Upper laminal cells were considered as those approximately 5 cells below the leaf apex. Only perichaetial branch leaves were measured as these are always present in collections and usually in fairer condition than leaves of the male branches. Plant size was scored as either small, medium or large based on leaf size and stem length. Descriptions of genera are based on the African species alone.

Mapping of specimens used GPS co-ordinate data from herbarium material to generate a distribution file in Google Earth (Google Inc., 2009) for each species. The individual .kml files where then exported and opened in QGIS (Team, 2012), where figures were generated using layers for topography and country outlines. Scales for maps vary depending on the size of the species distribution.

5.3. Taxonomic characters

Despite their reputation for being difficult to identify, and of being morphologically rather uniform (Fife, 1985; Liu et al., 2012), species of *Entosthodon sensu lato* usually exhibit distinctive characters, and once known, are rather easy to identify. Important characters/character suites are discussed below, highlighting the main variants that are useful in specimen identification.

Plant size

On the whole plants of *Amphoritheca* and *Entosthodon* are generally smaller in comparison to those of *Physcomitrellopsis*, *Fifeobryum* and *Funariella*, but exceptions do exist. In particular, *A. jamesonii* can produce long sterile branches and *E. lepervanchei*, *E. curvipes* and *E. zygolimbatus* produce gametophytes with bigger than average leaves. Overall plant size can vary greatly within a single population, and whilst most plants within a population appear to reach an aver-

age or maximum size, there are often some that only reach half of this average. These dwarf plants are often scattered amongst 'full' sized plants and may be the result of a nutrient or water limitation or possibly have a genetic basis. Generally, the length of stems is somewhere between 2 mm and 5 mm, and plant size is thus not often a useful discriminating character. The sterile branches of *A. jamesonii*, however, can exceed 10 mm and the gametophytes of *F. mayottensis* can be up to 25 mm in length making these species easy to recognize. In cross-section the stems are remarkably uniform (see Figure 5.1, no 1). Species may possess 1 or 2 layers of thicker–walled cortical cells but this tends to vary too much within species for it to be taxonomically useful.

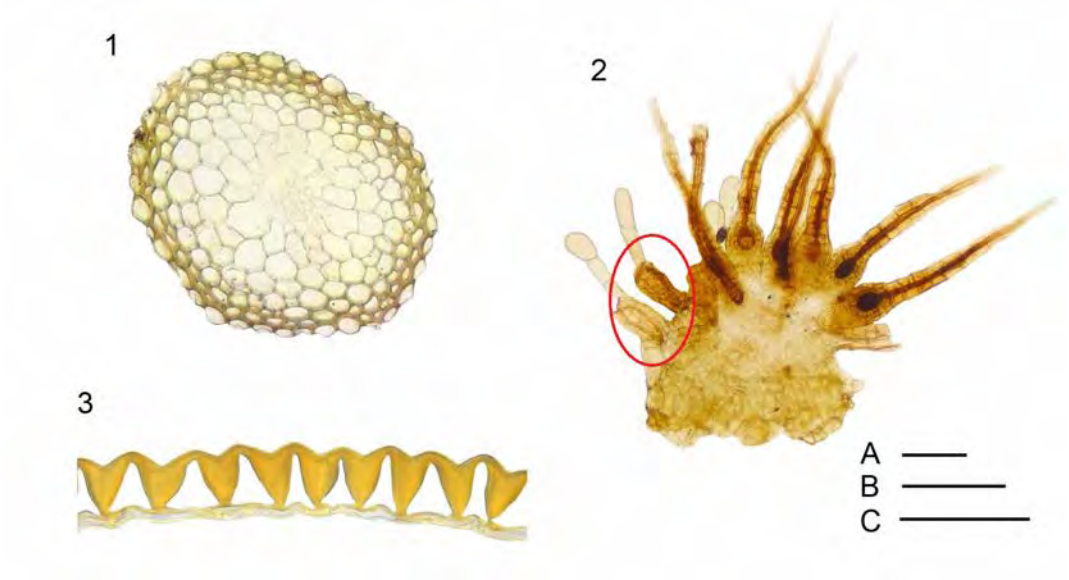

Figure 5.1: Stem cross-section - 1; synoicous infloresence (antheridia circled in red) - 2 and cross-section of exothecial cells - 3, in species of *Entosthodon s.l.*. Scale bars: A(1) = 125 µm; B(2) = 100 µm; C(3) = 50 µm.

Leaf morphology

In contrast to the fact that overall gametophyte morphology is relatively uniform across the family, the leaves of *Entosthodon s.l.* provide a rich source of taxonomic characters. These include shape, size, presence or absence of differentiated marginal cells, presence or absence of teeth on the margin, the nature of these teeth, costa length, costa anatomy, and the presence or absence of an arista.

The leaves of many species are oblong-obovate to spathulate and shortly acuminate. However, the leaves of *Amphoritheca jamesonii* are ovate lanceolate to subulate while those of *A. lindigii* are typically oblong-ovate to lanceolate. Within species shape can vary, often between ovate and elliptical or elliptical and obovate.

Measures of perichaetial leaf length fall largely within the 1.5–2.5 mm range. The large range of leaf sizes within most species limits its value as a taxonomic character. The perichaetial leaves directly surrounding the seta generally vary little in comparison to lower leaves, with the exception of size that usually decreases going down the stem. Perigonial leaves are on average ½ to ⅔ the size of the perichaetial leaves and usually of the same shape.

Marginal cells are often elongated and possess thickened cell walls, forming a distinct border, in *Entosthodon s.s.*, but such borders also occur in *Funariella*. These borders are typically 1–3 rows wide and are most prominent in the upper half of leaves. In many species these cells form teeth, which are often conspicuous even when leaves are dry. They have an immense value as taxonomic characters because presence or absence is easily and unambiguously determined.

Marginal teeth can also be formed by otherwise typical and undifferentiated cells that become inflated and bulge outwards. When these teeth are large and prominent they provide a good character for recognizing species. Such teeth are especially typical of *Fifeobryum* and *Physcomitrellopsis*, but also occur in some

species of *Funariella* and *Entosthodon s.s.* although they are never as pronounced as in the former genera.

Costa length is rather variable within and between species, but a useful character is provided by whether it ends below the apex or is excurrent. In some species, the ending of the costa may become ambiguous when it reaches as far as the apex and fuses with an arista or apiculus and in doing so appears excurrent, e.g. in *F. sebapala*. Inspection of multiple leaves should make it clear whether the costa is truly excurrent. As a taxonomic character it is best used to classify those species in which it is excurrent and for those where it ends below the leaf apex.

Few species of *Entosthodon* possess aristas and in some of those the presence or absence of an arista can vary, e.g. in *E. pocsii* and *E. pertenellus*, which makes it a tricky character for these species. In other species where the character is stable (e.g. it is uniformly present in *Funariella campylopodioides* and *Amphoritheca lindigii*) it is a more helpful taxonomic character.

Leaf cross-sections are not the most important character for determining species of *Entosthodon s.l.* and for the most part the anatomy of the leaf section seems to be invariant across the group. Only select species of *Amphoritheca* posses a single layer of adaxial cells in the costa while the remaining species in *Entosthodon s.l.* all possess 2 layers depending on the position of the leaf section. The size of the hydroid band varies significantly within species, between populations and across the leaf.

Size and shape of laminal cells

Laminal cells are never homogeneous in size and shape. Length increases towards the base of the leaf and the shape generally changes from rhomboidal-hexagonal near the upper portion of the leaves to uniformly rectangular near the base. As a taxonomic character neither size nor shape plays an important role

because of the low variability between species and the high variability within.

Rhizoid colour

Rhizoid colour varies from reddish-brown in species of *Funariella, Fifeobryum* and *Physcomitrellopsis* to distinctively cerise in *Entosthodon s.s.*. Colour, however, can be affected by age or decomposition of the plants which makes it an unreliable character.

Paraphyses

The shape of the terminal cells varies between globose, cylindrical and pyriform, often within species, see Figure 5.1 no. 2 for an example. As a result the taxonomic value of the paraphyses appears to be limited to recognizing members of the family.

Setae

Seta length varies significantly within species and is thus a relatively poor taxonomic character. In the extreme case where the seta is almost absent, i.e. *Physcomitrellopsis africana*, or is longer than 3 cm, i.e. *Entosthodon lepervanchei*, this may help to identify species.

With the exception of *Amphoritheca lindigii*, which has a distinctly papillose seta, the setae of all other species are smooth. Similarly for the twisting of the seta, only a single species, *Funariella spathulata*, has a seta which is twisted to the right (sometimes only in the upper-half) whilst in all other species they are twisted to the left.

Other features of the seta such as colour and shape can vary within species and are not reliable taxonomic characters.

Capsule size and shape

The most important aspect of capsule shape is symmetry. Within *Entosthodon s.l.* this varies from radially symmetric to zygomorphic. Most radially symmetric capsules are obovoid/pyriform but can also be oblong pyriform or clavate. The cleistocarpic capsule of *P. africana* stands out in the group in its globose to elliptical shape. Capsule size varies with gametophyte size which, depending on the situation, can be full sized or much smaller in dwarf plants.

Exothecial cells

The exothecial cells of *Entosthodon s.l.* are generally rhomboidal to spindle shaped, with conspicuous anticlinal thickening of the cell walls (see Figure 5.1, no 3). The shape of the cells, however, is not uniform in zygomorphic capsules and the concave side of the capsule is usually comprised of cells that are wider and shorter than the rest. The exothecial cells of *E. curvipes* are often much shorter and wider, with thicker anticlinal walls, than any other species of *Entosthodon s.l.*. The exothecial cells of *P. africana* are also different from other close relatives in being subquadrate to hexagonal in shape with no anticlinal thickening of the cell walls.

Operculum

Operculae of *Entosthodon s.l.* are mostly plano-convex. In *E. rhomboideus,* operculae can at times be conic and in *F. sulcata* the operculum is always conic. Cells of the operculum, when viewed from above, can be twisted anti-clockwise or not and this can vary within species. Twisting of the operculum cells appears to be related to the presence of a peristome and often its degree of development, though twisted cell patterns have been observed even when the peristome is rudimentary (e.g. in *E. limbatus*).

Peristome

The peristome of *Entosthodon s.l.* varies enormously, forming a grade in development from absent in some species to having both the endostome and exostome well-developed in others. Presence or absence is an important taxonomic character. However, care should be taken when determining whether the peristome is truly absent as the teeth are sometimes fugacious and have a tendency to be missing in older capsules.

The degree to which the peristome is developed can vary enormously within species. Some species may contain populations with peristome teeth and others where the peristome is absent. Likewise, the complexity of the peristome may vary - for example a rudimentary exostome may be present in species that are typically gymnostomous. When both endostome and exostome are present, the exostome is always better developed than the endostome. Most often this variation occurs between populations, but can occur within the same population.

The exostome teeth are most commonly straight but can be sigmoidal in shape when larger and well developed. The teeth are usually striate and trabeculate. Many species possess teeth with fine papillae and in a few species these papillae are much larger and variable. Ornamentation is not stable or variable enough to be used taxonomically. When the exostome is rudimentary, the teeth may form rounded stubs or narrow teeth irregular in shape or individual teeth may be seemingly comprised of disconnected segments.

Within some species the exostome is more variable than in others while the presence or absence of the exostome is fairly constant across most species, with the exception of some like *Funariella urceolata* and *Fifeobryum longicollis*. The length of exostome teeth varies greatly across species depending on the overall size of the capsule and the degree to which the peristome is developed. In smaller species, such as *E. pocsii*, the exostome teeth are up to 175 μm in length while

in comparison the teeth of larger species like *F. spathulata* may exceed 300 µm in length.

The endostome is similarly variable and most often absent or rudimentary and consisting only of shorter and wider hyaline to pale-yellow teeth that are usually finely papillose.

Prostome

A rudimentary prostome is present in only two sister species, *E. claudineae* and *E. lepervanchei*. The prostome teeth are always wider than long, striate, and with rounded apices.

Calyptra

In general, the cucullate, rostrate calyptra does not vary across members of *Entosthodon s.l.*. However, *Physcomitrellopsis africana*, has a calyptra that completely encloses the capsule, is mitrate, rostrate and with papillose cells.

Spores

Fife (1985) was the first to study spore morphology in the hope that it could be used to clarify subgeneric relationships within *Entosthodon*. However, finding that the spores were the most variable in the family, he was unable to use them to clarify subgeneric relationships. The spores of *Entosthodon s.l.* comprise a number of important taxonomic characters including size, shape, ornamentation and presence/absence of a trilete scar.

Spore size in the majority of species is typically in the range of 28–38 µm. However, some species, for example *E. bergianus*, can produce spores that can approach twice the average size (*ca.* 55 um) but this is apparently rare. Within species, spore size usually varies by *ca.* 10 µm among populations.

Spore shape is generally tetrahedral, but in *Funariella* the spores are often collapsed so that they resemble metal bottle caps. The Macaronesian species *E.*

kroonkurk (=crown caps) is named after this.

Fife (1985) classified spore ornamentation into four basic patterns: verrucate-bullate, smooth, reticulate, and baculate-insulate. Ornamentation is a difficult character to use taxonomically because it tends to vary within species, is often not greatly variable between closely related species, ornamentation may be homoplasious and the relationships between different ornamentation patterns is not understood. Trilete scars are found in *Funariella, Fifeobryum, Physcomitrellopsis* and *Amphoritheca* and are absent from *Entosthodon s.s.*. Limited perine deposition is probably what allows the mark to persist although *A. productus* may be the exception to this with its obvious trilete scar and thick perine layer (Fife 1985, Fife & Seppelt 2001).

Sexual condition

At this stage sexual condition has proven of little value to the taxonomy of *Entosthodon s.l.*, however, at a family level the character might still prove of some value once *Physcomitrium* and its allied genera are better understood. For a discussion of the Polyoicous condition frequently observed in *Entosthodon s.l.* see Section 6.1.1.

5.4. Taxonomic Treatment

5.4.1. Key to the African species of *Entosthodon s.l.*

1. Leaves 2–2.5 x 0.7–1.5 mm, costa consistently percurrent or slightly excurrent, marginal cells forming border 1–2 cells thick, toothed in upper ⅓, perigonia only .....*Funariella mayottensis*

1. All characters different 2

2. Sporphytes immersed .....*Physcomitrellopsis africana*

2. Sporphytes exserted 3

3. Capsules radially symmetric or weakly zygomorphic, eperistomate or peristomate 4

3. Capsules strongly zygomorphic, gibbous, peristomate 20

4. Peristome present 5

4. Peristome absent 13

5. Leaves strongly bordered by 1–3 rows of narrower, thicker-walled cells ....*Entosthodon limbatus*

5. Leaves not or weakly bordered 6

6. Leaves toothed in upper-half 7

6. Leaves entire 9

7. Costa excurrent .....*Fifeobryum longicollis*

7. Costa ending below leaf apex 8

8. Marginal cells inflated, forming obtuse teeth, operculum short-conic, spores finely papillose or papillose-lirate .....*Entosthodon rhomboideus*

8. Marginal cells narrower, forming toothed border, operculum plano-convex, spores verrucate-lirate to reticulate .....*Entosthodon limbatus*

9. Spores collapsed .....*Funariella succuleata*

9. Spores not collapsed 10

10. Spores bacullate-insulate .....*Funariella sebapala*
10. Spores finely verrucate-lirate or verrucate-lirate to reticulate 11
11. Exostome teeth verrucate-lirate, finely papillose and striate, not hyaline above 12
11. Exostome teeth striate, becoming hyaline in upper ⅓ ....*Entosthodon bergianus*
12. Spores finely papillose-lirate .....*Entosthodon pocsii*
12. Spores verrucate lirate to reticulate .....*Entosthodon limbatus*
13. Leaves strongly bordered by 1–3 rows of narrower, thicker-walled cells ....*Entosthodon borbonicus*
13. Leaves not or weakly bordered 14
14. Seta papillose .....*Amphoritheca lindigii*
14. Seta smooth 15
15. Leaves ovate lanceolate to subulate .....*Amphoritheca jamesonii*
15. All other leaf shapes 16
16. Costa excurrent 17
16. Costa ending below leaf apex 19
17. Leaves less than 2 mm long .....*Entosthodon pertenellus*
17. Leaves longer than 2 mm 18
18. Leaves lingulate to oblong-obovate .....*Funariella urceolata*
18. Leaves elliptical to obovate or spathulate ....*Funariella campylopodioides*
19. Leaves in cross-section with one adaxial and one abaxial layer of large cells surrounding a central stereid group .....*Amphoritheca gymnostoma*
19. Leaves in cross-section with one adaxial and two abaxial layer of large cells surrounding a central stereid group .....*Funariella clavata*
20. Leaves strongly bordered by 1–3 rows of narrower, thicker-walled cells ..21

20. Leaves not or weakly bordered 23
21. Seta longer than 20 mm .....*Entosthodon lepervanchei*
21. Seta less than 20 mm long 22
22. Exostome teeth straight or sigmoidal to 460 um long, spores finely verrucate-lirate .....*Entosthodon curvipes*
22. Exostome teeth straight to 230 um long, spores coarsely verrucate .....*Entosthodon zygolimbatus*
23. Seta twisted clockwise in upper half .....*Funariella spathulata*
23. Seta twisted anti-clockwise throughout 24
24. Leaves acuminate, arista present 25
24. Leaves short acuminate to apiculate, arista usually absent 27
25. Spores 12–23 .....*Funariella sulcata*
25. Spores greater than 25 µm 26
26. Leaves bordered by a single row of cells and serrate in upper-half, spores verrucate-lirate to reticulate .....*Entosthodon heddersonii*
26. Leaves not bordered by a single row of cells or serrate in upper-half, spores smooth to minutely verrucose, collapsed .....*Funariella chevalieri*
27. Rudimentary prostome present .....*Entosthodon claudineae*
27. Rudimentary prostome absent .....*Entosthodon cameruniae*

5.4.2. *Amphoritheca* Hampe

Amphoritheca Hampe in Triana & Planchon, Ann. Sci. Nat., Bot. sér. 5, 3: 339. 1865. *Entosthodon sect. Amphoritheca* (Hampe) Mitt., J. Linn. Soc., Bot. 12: 242, 243. 1869.–LECTOTYPE: *Amphoritheca lindigii* Hampe, Triana & Planchon, Ann. Sci. Nat., Bot., sér. 5, 3:341 (1865). Of the five species originally published by Hampe under Amphoritheca only two names are currently accepted: *A. jamesonii* (Taylor) Hampe and *A. lindigii* Hampe, and both fit the current phylogenetic concept of the genus, see Chapter 2. Given that *Amphoritheca* was originally erected for species of *Entosthodon* lacking a peristome and that in both *A. lindigii* and *A. jamesonii* a peristome may in fact be present, my choice of the lectotype, in this instance, is arbitrary.

Synonyms:

Funaria sect. Trigonomitria M.Fleisch. ex Broth., Nat. Pflanzenfam. [Engler & Prantl] I(3): 522. 1903. *Entosthodon subg. Trigonomitria* (M.Fleisch ex. Broth.) M. Fleisch, Musci Buitenzorg 2: 483. 1904. *Entosthodon sect. Trigonomitria* (M.Fleisch ex. Broth.) M.Fleisch, Musc. Buitenzorg 4: 1727. 1923.–TYPE: *Entosthodon mittenii* Dozy & Molk.

Plants small to large, gregarious, pale-green to green. Stems reddish-brown, to 10 mm, branching multiple times by sub-perigonial innovation and/or by dichotomy, sometimes with sterile branches to 10 mm, in cross-section with 1–2 layers of thick-walled, reddish cortical cells, a hyalodermis and a central strand, rhizoids reddish-brown. Leaves erect, scarcely contorted dry, concave, ovate-lanceolate to oblong-obovate, subulate, 1.3–2.1 x 0.3–0.8 mm, acuminate or short

apiculate, arista present or absent, margins entire or weakly serrate in upper ⅓; cells of upper lamina thick or thin-walled, rectangular, occasionally pentagonal or oblong hexagonal, 22–63 x 13–25 µm; basal cells rectangular, thinner-walled, longer and laxer, (35)42–175 x 15–40(48) µm; marginal cells undifferentiated; costae ending below apex or extending into base of arista but never fusing with it, in cross-section with one adaxial and one abaxial layer of large cells surrounding a central stereid group. Axillary-hairs present, hyaline, multicellular, uniseriate, apical cell largest and with rounded end walls. Polyoicous. Perigonia single, terminating primary shoot, synoicous shoots arising by sub-perigonial innovation, protogynous. Paraphyses club-shaped. Setae 2–25 mm long, reddish-yellow to reddish-brown, twisted anti-clockwise, smooth or papillose, straight. Capsules erect to weakly inclined, radially symmetric, oblong pyriform, 0.9–1.8 x 0.4–0.9 mm, reddish-brown at maturity, constricted below mouth when dry with neck ½ length of capsule, neck sulcate; mouth ⅔ to ¾ diameter of capsule, transverse; exothecial cells with obscure lumina, 32–75 x 10–20 µm, pentagonal to oblong-hexagonal, in cross-section with strongly cuneate anticlinal walls, 2–5 rows of oblate cells at mouth. Opercula plano-convex, to convex, cells not twisted. Peristome single or absent; exostome teeth rudimentary or absent. Spores tetrahedral, 25–35 µm, verrucate-lirate or coarsely verrucate-bullate, trilete scars present or absent. Calyptrae cucullate, rostrate.

The genus is represented by three species in Africa, two of these were only recently recorded by Wilding and Hedderson (2011) for the region. In the Southern Hemisphere, the genus is defined by the presence of one adaxial and one abaxial layer of large cells surrounding a central stereid group in cross-sections of the costa.

Amphoritheca gymnostoma (Dixon) N. Wilding *comb. nov.* Basionym: *Funaria gymnostoma* Dixon, S. African J. Sci. 18: 318 (1922).–TYPE: SOUTH AFRICA. KwaZulu–Natal, Goodoo Pass, Jan. 1918, *Wager s.n.* (BM, lectotype!, designated here; isolectotype in PRE!). I have chosen the BM specimen to serve as the lectotype because of Dixon's association with BM and therefore the likelihood that he would have seen this specimen over the isotype in PRE.

Illustration: Figure 5.3.

Plants small, light–green. *Stems* reddish–brown, to 3 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. *Leaves* erect–spreading, ovate–lanceolate to oblong–obovate, 1.3–2.1 x 0.5–0.8 mm, plane, short acuminate to apiculate, entire to weakly serrate in upper ⅓, arista absent; *cells of upper lamina* quadrate to oblong–hexagonal, 32–55 x 20–25 µm; *basal* 100–175 x 27–40(48) µm; *marginal cells* undifferentiated; *costae* ending below apex.

Polyoicous. *Setae* 3–9 mm long, straight, smooth, yellowish–brown. *Capsules* erect to inclined, radially symmetric, oblong-pyriform, 1.2–1.4 x 0.4–0.5 mm, weakly constricted below mouth when dry, yellow to reddish–brown at maturity, with a well differentiated neck *ca.* ½ total length of capsule; *mouth* transverse *ca.* ⅔ diameter of capsule; *exothecial cells*, 50–75 x 10–15 µm, in cross-section with thick, strongly cuneate anticlinal walls, *ca.* 3–4 rows of oblate cells at mouth. *Opercula* plano–convex, cells not twisted. *Peristome* absent. *Spores* 25–28 µm, tetrahedral, verrucate-lirate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Amphoritheca gymnostoma is most easily confused with *F. urceolata* as the two bear some similarity at first glance and are known to co-occur. *Amphoritheca gymnostoma* is, however, about half as big as *F. urceolata* and its spores are smaller and finely papillose vs. low baculate to verrucate–lirate in *F. urceolata*.

Habitat and Distribution

The species is known from the NE parts of South Africa (Figure 5.2). *Amphoritheca gymnostoma* has been collected on south–facing slopes in open grassland at 850 m and probably at a higher altitude along the Goodoo Pass though little locality information is given by Wager for the type.

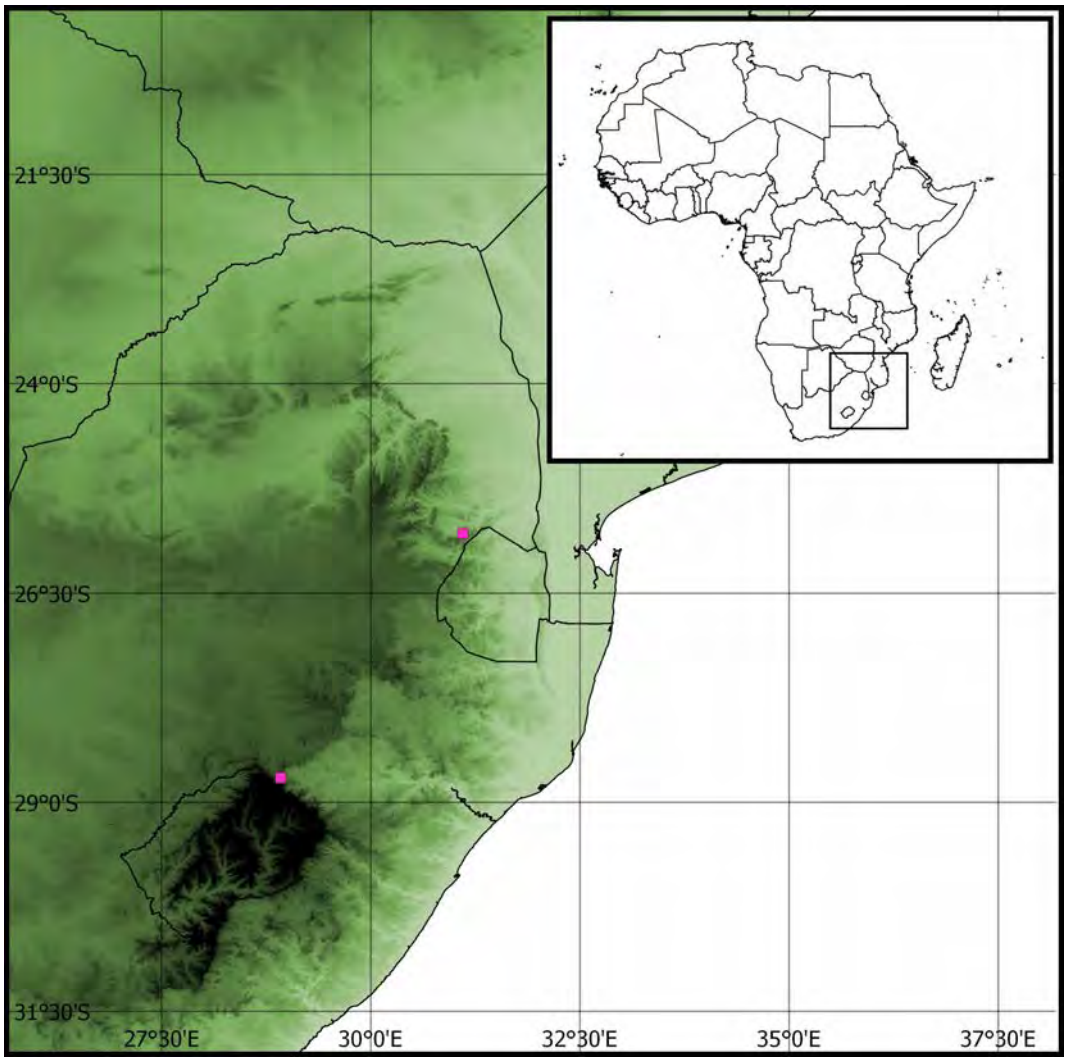

Figure 5.2: Distribution of *A. gymnostoma* in Africa.

Specimens Examined

SOUTH AFRICA. KwaZulu–Natal, Goodoo Forest, *Wager 11672* (PRE, MO); Mpumalanga, Barberton, E.G.H. Oliver 7172, 10/4/1972 (PRE).

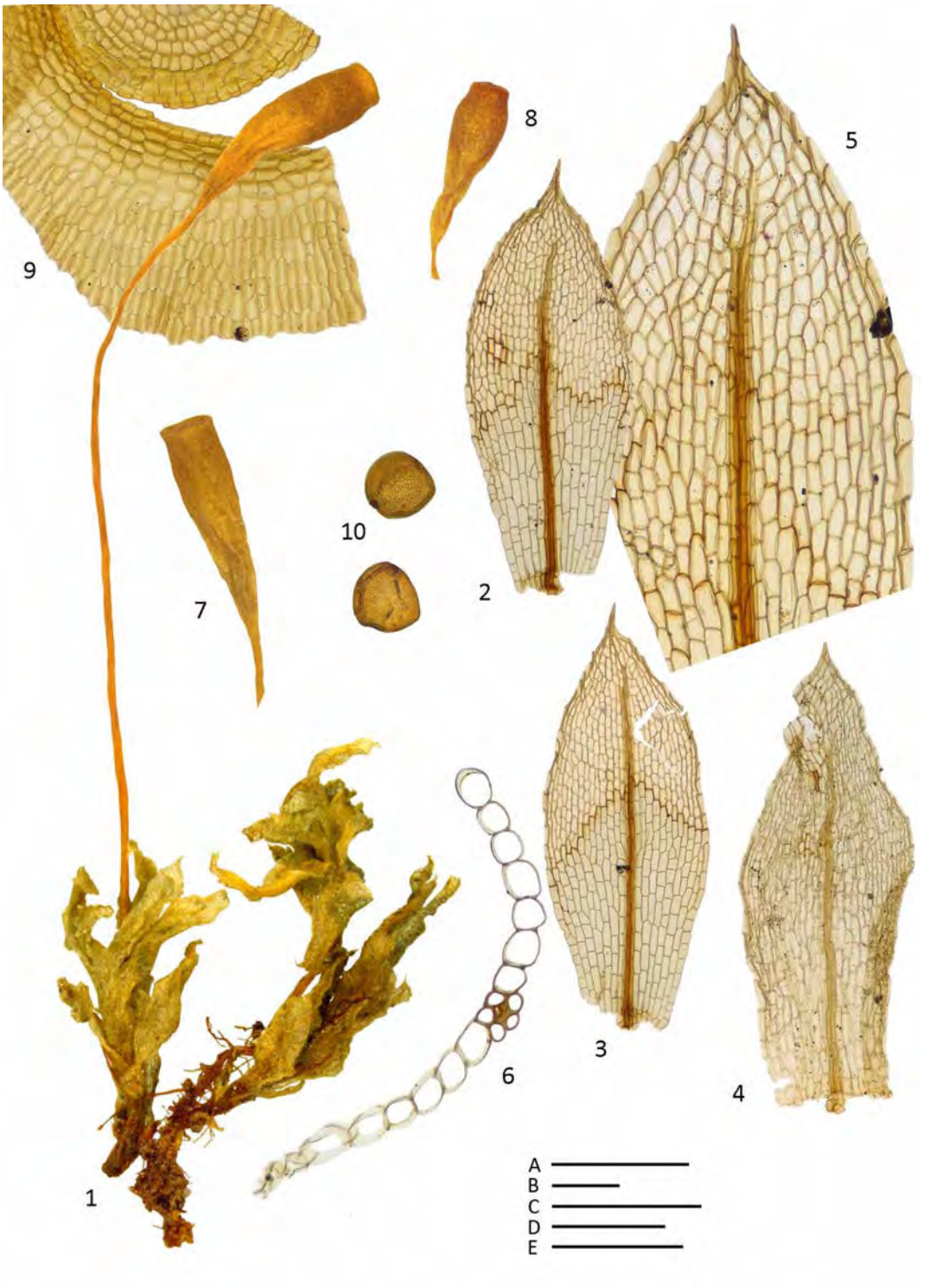

Figure 5.3: *Amphoritheca gymnostoma*. 1. Habit, dry (*Wager 11672*, PRE); 2–4. Leaves (2, 3 – *E.G.H. Oliver 7172*, PRE; 4 – as for 1); 5. Leaf apex (as for 2 & 3); 6. Leaf cross-section (as for 2 & 3); 7, 8. Capsule, dry (as for 1); 9. Capsule mouth, operculum & exothecial cells (as for 2 & 3); 10. Spores (as for 1). Scale bars: A (2–4) = 500 µm; B (5, 9) = 100 µm; C (1, 7, 8) = 1 mm; D (6) = 100 µm; E (10) = 50 µm.

Amphoritheca jamesonii (Taylor) Hampe, Ann. Sci. Nat. Bot., sér. 5, 3: 340 (1865). *Physcomitrium jamesonii* Taylor, London J. Bot. 6: 329 (1847). *Entosthodon jamesonii* (Taylor) Mitt., Hooker's J. Bot. Kew Gard. Misc. 3: 354. 1851.–TYPE: ECUADOR. Pichincha: Nov. 1846, *Prof. W. Jameson* (FH-TAYL., holotype).

Synonyms:

Gymnostomum acidotum Taylor, London J. Bot. 7: 279 (1848), *fide* Fife (1987). *Entosthodon acidotus* (Taylor) Müll. Hal., Syn. Musc. Frond. 2: 547 (1851).–TYPE: ECUADOR. On Pichincha, near the limits of perpetual snow, 5 Jul. 1847, *Prof. W. Jameson* (FH-TAYL., holotype).

Entosthodon mittenii Dozy & Molk., Bryol. Jav. 1: 32, pl. 23 (1855), *fide* Fife (1987).–TYPE: JAVA. Presumably collected by Teysmann (H-BR).

Entosthodon mandonii Schimp. ex Britt., Bull. Torrey Bot. Club 23:482 (1896), *fide* Fife (1987).–TYPE: BOLIVIA. Ancouma, *Mandon 1645* (NY, lectotype (Fife (1987))).

Entosthodon apiculatus Schimp. ex Britt., Bull. Torrey Bot. Club 23:482 (1896), *fide* Fife (1987).–TYPE: BOLIVIA. Ancouma, *Mandon 1646* (NY-JAEG).

Entosthodon subtilis Müll. Hal., Nouvo Giorn. Bot. Ital. n.s. 4:9 (1897), *fide* Fife (1987).–TYPE: BOLIVIA. Cochabamba: Prope Choquecamata, 10,000-12,000 ft., Jun. 1889, *Germain s.n.* (NY, H-BR, G).

Funaria monticola Broth., in Warburg, Monsunia 1: 44 (1900), *fide* Fife (1987).–TYPE: INDONESIA. Sulawesi (Celebes). Pik von Bonthain, *O. Warburg s.n.* (H-BR, lectotype (Fife (1987)); isolectotypes in FH-FLEISCH., H-BR).

Entosthodon subulatus E.B.Bartram, Lloydia 5: 259, pl. 1, fig. 12 (1942), *fide* Fife (1987).–TYPE: INDONESIA. Irian Jaya (West New Guinea). E. Wilhelmina, top, wet limestone near waterfall, 3850 m, Sep. 1938, *L. J. Brass &*

E. Myer-Drees 10365 (MICH).

Illustrations: Figure 5.5.

Plants small to large, light-green. *Stems* reddish-brown, to 4 mm high, branching by sub-perigonial innovation or by dichotomies, producing sterile branches to 10 mm, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish-brown. *Leaves* erect, ovate-lanceolate to subulate, 1.4–1.8 x 0.3–0.6 mm, concave, acuminate, entire, arista absent; *cells of upper lamina* rectangular 28–48(55) x 13–15 µm, often with thickened cell walls; *basal* (35)50–138 x 15–30 µm; *marginal cells* narrower; *costae* ending below apex.

Polyoicous. *Setae* 15–25 mm long, straight, smooth, reddish-brown. *Capsules* erect or weakly inclined, slightly zygomorphic, oblong-pyriform, 1.5–1.8 x 0.7–0.9 mm, constricted below mouth when dry, reddish-brown at maturity, with a well differentiated neck *ca.* ½ total length of capsule; *mouth* transverse, *ca.* ¾ the diameter of capsule; *exothecial cells* 48–70 x 10–20 µm, in cross-section with thick, strongly cuneate anticlinal walls, *ca.* 3–5 rows of oblate cells at mouth. *Opercula* plano-convex, cells not twisted. *Peristome* single and rudimentary or absent; *exostome teeth* if present, poorly developed. *Spores* 25–35 µm, tetrahedral, coarsely verrucate bullate, trilete scars often visible. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Amphoritheca jamesonii is easily recognized by virtue of its erect, ovate-lanceolate to subulate leaves, the cells of which are usually thick-walled. The species is further recognized by the presence of long, sterile branches which may exceed the

sexual shoots in length.

Habitat and Distribution

Amphoritheca jamesonii has a pantropical distribution, and is known from Central and South America, Malesia and Africa. In Africa the species is recorded from afro-alpine habitats in Ethiopia, Kenya, Tanzania and Réunion Island (Figure 5.4). On Réunion Island the species occurs at elevations between 2400 m and 2800 m and on the continent at higher elevations between 3150 m and 3900 m. *Amphoritheca jamesonii* is frequently associated with wet-humusy environments such as boggy stream-sides or dripping cliffs.

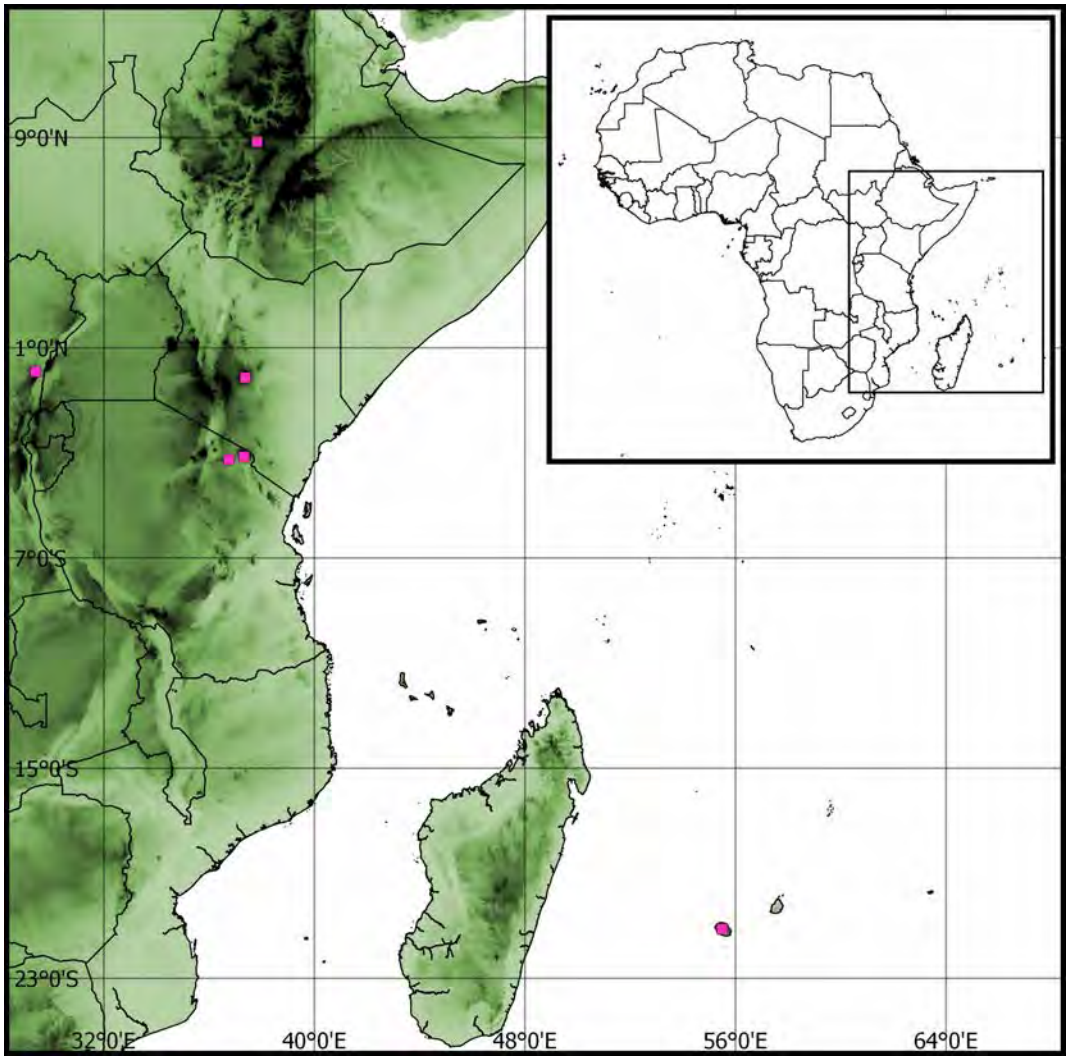

Figure 5.4: Distribution of *A. jamesonii* in Africa.

Note

In comparison to South American specimens, the African plants have smaller leaves, the upper-laminal cells are shorter, cell walls are more highly thickened and cells are generally more quadrate throughout.

Specimens Examined

DEMOCRATIC REPUBLIC OF THE CONGO. Virunga, *De Sloover 13201* (EGR);

ETHIOPIA. Shewa, *D.A. Petellin 11–2*, 14/10/1990 (MO).

KENYA. Mnt Kenya, *P. Kuchar B8705*, 2/10/1979 (MO).

RÉUNION ISLAND (FRANCE). Piton de la Fournaise, *T.A.J. Hedderson 15811*, 1/12/2004 (BOL), Cilaos, *A. Szabo 9640/CD*, 11/6/1996 (BOL, EGR), *N. Wilding 174*, 3/10/2011 (BOL). Pas de Bellecombe, *N. Wilding 65, 70,* 25/4/2010 (BOL); Salazie, *G. Kis 9422/AD*, 24/8/1994 (BOL, EGR).

TANZANIA. Arusha N.P.,*T. Pócs & Helsinki Univ. Bot. Dept. 88094/BH*, 26/5/1988 (BOL, EGR), Mt. Meru, *T. Pócs, R. Ochyra & H. Bednarek–Ochyra, 88152/AG, 88152/BJ*, 24/6/1988 (BOL, EGR).

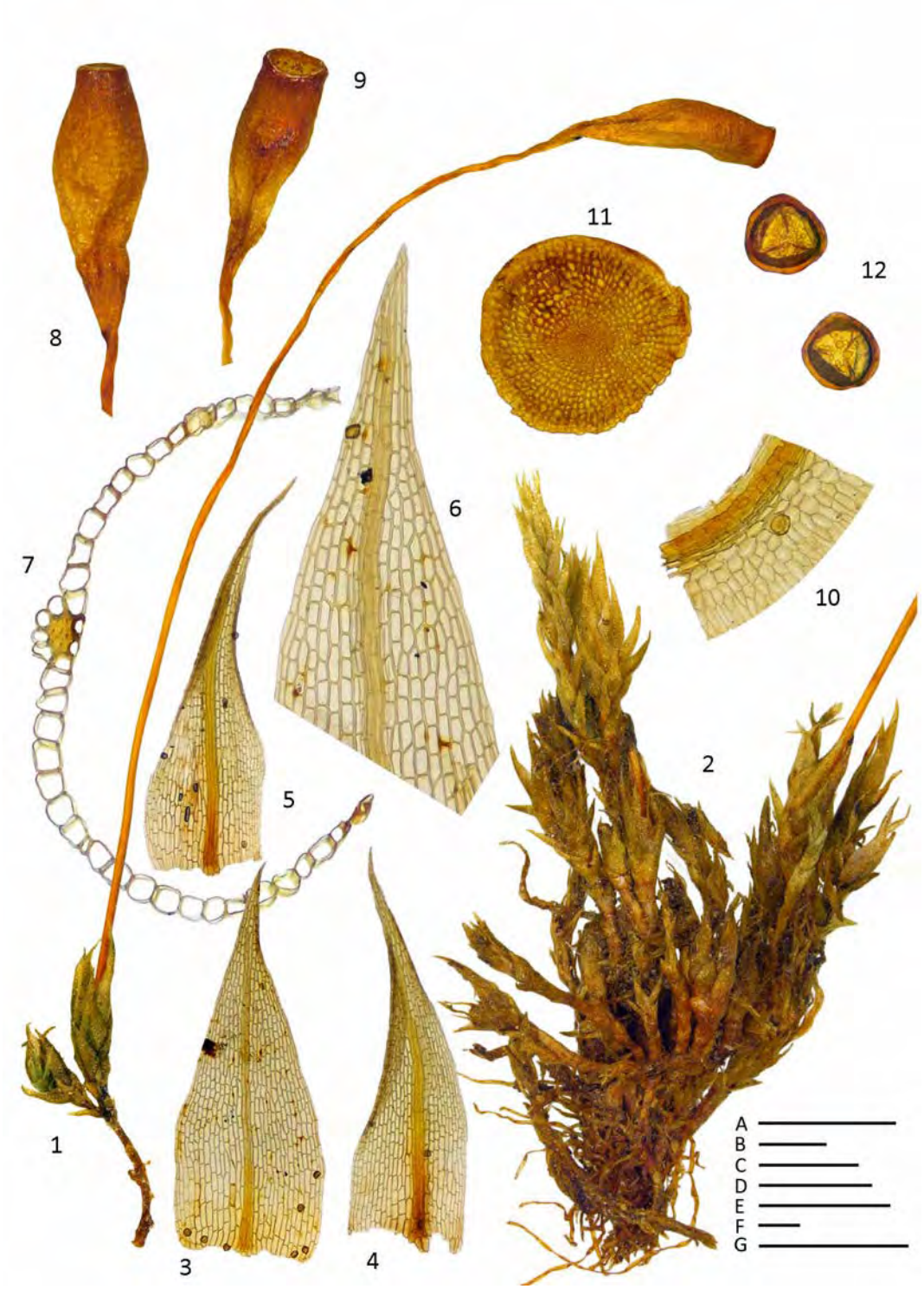

Figure 5.5: *Amphoritheca jamesonii*. 1, 2. Habit, dry (*N. Wilding 174*, BOL); 3–5. Leaves (3 – *Szabo 9460CD*, EGR; 4, 5 – *T.A.J. Hedderson 15811*, BOL); 6. Leaf apex (as for 3); 7. Leaf cross-section (as for 1 & 2); 8, 9. Capsule, dry (8 – *T. Pócs & Helsinki Univ. Bot. Dept. 88094/BH*, BOL; 9 – as for 1 & 2); 10. Capsule mouth & exothecial cells (as for 1 & 2); 11. Operculum (*De Sloover 13201*, EGR); 12. Spores (as for 1 & 2). Scale bars: A (3–5) = 500 µm; B (6, 10) = 100 µm; C (1, 2) = 1 mm; D (7) = 100 µm; E (12) = 50 µm; F (11) = 100 µm; G (8, 9) = 1 mm.

Amphoritheca lindigii Hampe, Triana & Planchon, Ann. Sci. Nat. Bot. sér. 5, 3: 341 (1865). *Entosthodon lindigii* (Hampe) Mitt., J. Linn. Soc. Bot. 12: 243 (1869).–TYPE: COLOMBIA (Nova Granata). Bogotá, Pacho, Jul. 1863, *A. Lindig s.n.* (BM–HAMPE, lectotype (Fife (1987)); isolectotypes in BM, NY–JAEGER; probable isolectotype in H–BR).

Synonyms:

Entosthodon papillosus Britt., Bull Torrey Bot. Club 23: 483 (1896), "*papillosum*," hom. Illeg., non *E. papillosus* Müll. Hal. 1882. *E. soratensis Paris*, Index Bryol. Suppl. 142 (1900).–TYPE: BOLIVIA. Sorata, 10,000 ft., Feb. 1886, *H. H. Rusby 3131* (NY, holotype!).

Entosthodon verrucosus Müll. Hal., Nuovo Giorn. Bot. Ital. n.s. 4: 10 (1897), *fide* Fife (1987).–TYPE: BOLIVIA. Cochabamba: Prope Choquecamata, 10,000–12,000 ft., Jun. 1889, *Germain s.n.* (H–BR, lectotype (Fife (1987))).

Illustrations: Figure 5.7.

Plants small, light–green. *Stems* reddish-brown, to 3 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. *Leaves* erect, oblong to ovate–lanceolate, 1.3–1.7 x 0.4–0.7 mm (including arista), concave, acuminate, entire, aristate, arista to 600 µm; *cells of upper lamina* rectangular, occasionally pentagonal, rarely hexagonal, 22–63 x 17–20 µm; *basal* 42–130 x 17–23 µm; *marginal cells* undifferentiated; *costae* ending below apex or extending into base of arista but never fusing with it.

Polyoicous. *Setae* 2–4 mm long, straight, stout, papillose, reddish–orange. *Capsules* erect, radially symmetric, oblong–pyriform, 0.9–1.4 x 0.4–0.5 mm, constricted below mouth when dry, reddish–brown at maturity, with a well dif-

ferentiated neck *ca.* ½ total length of capsule; *mouth* transverse, *ca.* ⅔ diameter of capsule; *exothecial cells* 32–50 x 10–18 µm, in cross-section with thick, strongly cuneate anticlinal walls, 2–3 rows of oblate cells at mouth. *Opercula* plano–convex, cells not twisted. *Peristome* absent or immature. *Spores* immature in the single African collection (spores from Andean material are reported as 25–35 µm, coarsely bullate with trilete scars). *Calyptrae* cucullate, rostrate.

Diagnostic Features

Amphoritheca lindigii is easily recognized by its papillose seta, a feature unique among the Funariaceae.

Habitat and Distribution

Amphoritheca lindigii is known from a single population on the island of Grande Comore in the western Indian Ocean (Figure 5.6). It is otherwise known from the Andes and Central America, where it was, until recently, considered endemic to the region. The species was collected in *Erica* dominated vegetation on Grande Comore at 1900 m.

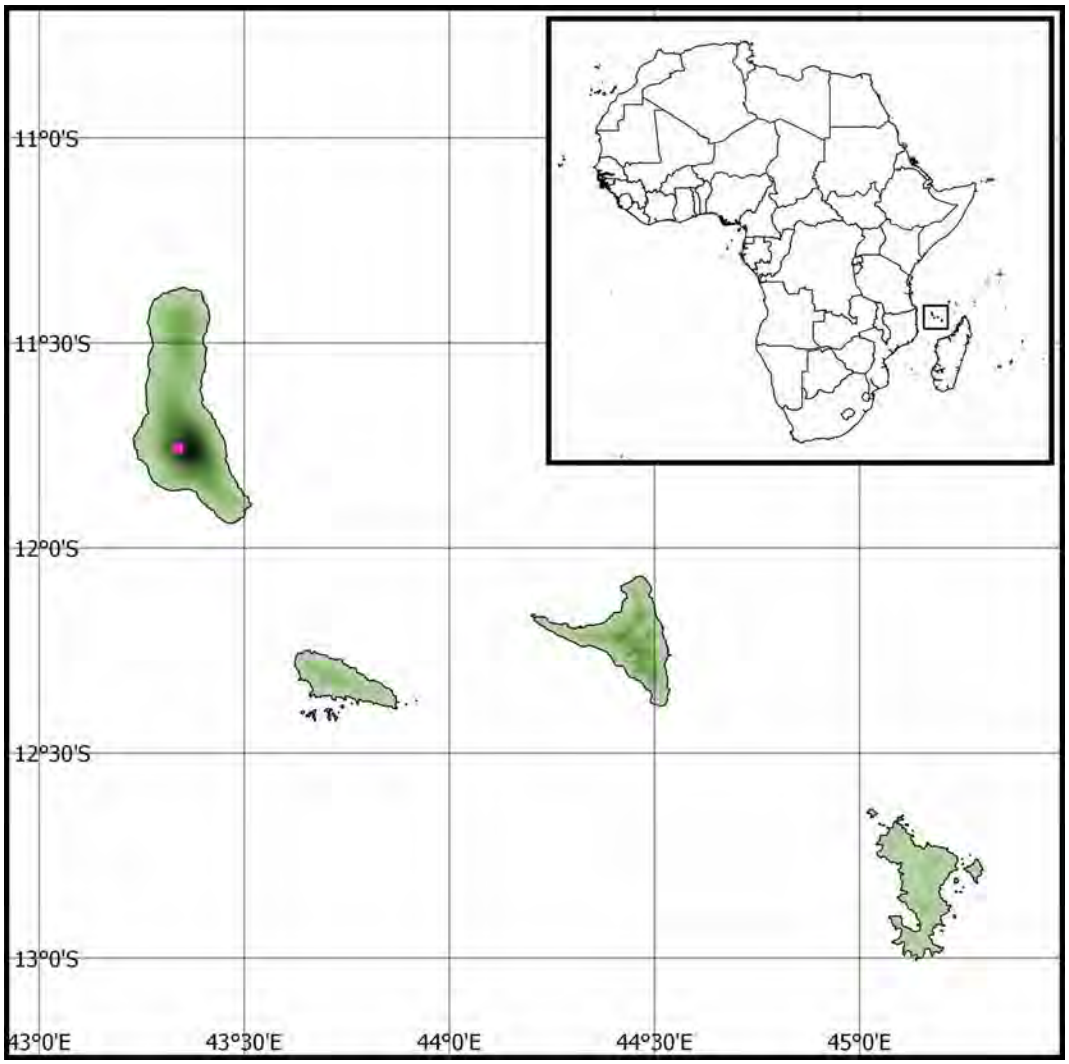

Figure 5.6: Distribution of *A. lindigii* in Africa.

Specimens Examined

COMOROS. Grande Comore, Karthala Forest. *T.A.J. Hedderson 16786, 16805,* 26/5/2008 (BOL).

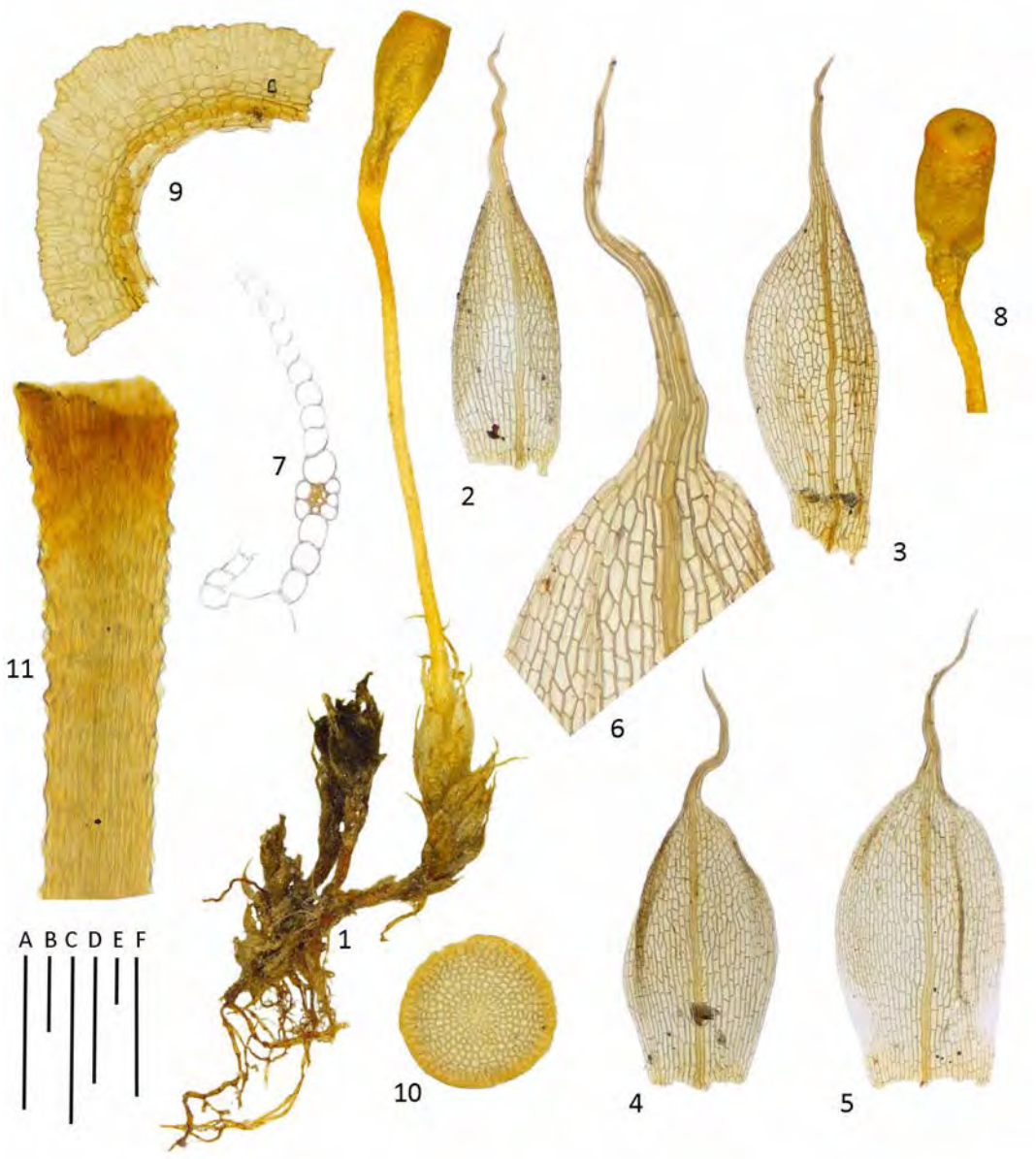

Figure 5.7: *Amphoritheca lindigii.* 1. Habit, dry; 2–5. Leaves; 6. Leaf apex; 7. Leaf cross-section; 8. Capsule, dry; 9. Capsule mouth & exothecial cells; 10. Operculum; 11 Seta. All from: *T.A.J. Hedderson 16805*, BOL. Scale bars: A (2–5) = 500 µm; B (6, 9, 11) = 100 µm; C (1) = 1 mm; D (7) = 100 µm; E (10) = 100 µm; F (8) = 500 µm.

5.4.3. *Entosthodon* Schwägr.

Entosthodon Schwägr., Spec. Musc. Suppl. 2(1): 44. 1823. *Physcomitrium sect. Entosthodon* (Schwägr.) Müll. Hal., Linnaea 18: 696. 1844. *Funaria subg. Entosthodon* (Schwägr.) Lindb. Musci Scand. 18. 1879. *Funaria sect. Entosthodon* (Schwägr.) Braithw., Brit. Moss Fl. 2: 130. 1890. *Entostodon* Schwägr. *ex* Hornsch., Flora 8 (2 Erg.): 13. 1825. Invalid, orthographic variant. *Entothodon* Schwägr. *ex* Brid., Bryol. Univ. 2: 78. 1827. Invalid, orthographic variant.–TYPE: *Entosthodon attenuatus* (Dicks.) Bryhn. Kongel. Norske Vidensk. Selsk. Skr. (Trondheim) 1908(8): 25 (1908).

Synonyms:

Bergia Fürnr., Flora 12 (2 Erg.): 26. 1829.–TYPE: *Weissia bergiana* Hornsch.

Funaria sect. Exannulatae Kindb., Eur. N. Amer. Bryin. 2: 329, 332. 1898.

Funaria sect. Euentosthodon Broth., Nat. Pflanzenfam. [Engler & Prantl] I(3): 522. 1903.

Entosthodon sect. Euentosthodon Müll. Hal., J. Linn. Soc., Bot. 12: 243. 1869. *nom. Illeg.*

Funaria sect. Leiolecythis Müll. Hal., Gen. Musc. Fr. 106. 1900. *nom. Illeg.*

Plants small to medium, gregarious, pale green to green. Stems reddish-brown, to 5 mm, branched at least once by sub–perigonial innovation, in cross-section with 1–3 layers of thick-walled, reddish cortical cells, a hyalodermis and a central strand, rhizoids reddish-brown or cerise. Leaves erect–spreading, little contorted to contorted when dry, concave or plane, oblong–obovate to spathulate, elliptical, or ovate, less frequently ovate lanceolate, (0.75)1.2–3.8 x 0.4–1.9(2.7)

mm, usually short acuminate, sometimes cuspidate, margins entire to toothed or serrate in upper–half, arista present or absent; cells of upper lamina usually thin–walled, rhomboidal to oblong–hexagonal, (22)30–95(113) x (10)15–38(45) µm; basal cells rectangular, thinner-walled, longer and laxer, (37)50–200(275) x (15)22–50(68) µm; marginal cells forming a border 1 to 3 rows wide or undifferentiated, often projecting in upper–half of leaf; costae ending well below apex to excurrent–aristate, in cross-section with two adaxial and one abaxial layer of large cells surrounding a central stereid group. Axillary-hairs present, hyaline, multicellular, uniseriate, apical cell largest and with rounded end walls. Polyoicous. Perigonia single, terminating primary shoot, synoicous shoots arising by sub–perigonial innovation, protogynous. Paraphyses club–shaped. Setae 2.5–30(40) mm long, red or reddish-brown, sometimes yellow, twisted anti-clockwise, smooth, rarely polysetous, straight, slightly curved or curved. Capsules erect or inclined, radially symmetric or zygomorphic, gibbous, pyriform, oblong-pyriform or oblong-obovoid, 1–2.5(4) x 0.4–0.9(1.2) mm, usually reddish-brown at maturity, constricted below mouth when dry with neck ¼ to ½ length of capsule, neck sulcate; mouth ⅔ to equal diameter of capsule, transverse or oblique; exothecial cells with obscure lumina, 28–70 x 10–25(28) µm, pentagonal to mostly oblong–hexagonal, in cross-section with strongly cuneate anticlinal walls, 2–8 rows of oblate cells at mouth. Opercula plano-convex, infrequently conic or short–conic, cells not twisted or twisted anti-clockwise from above. Peristome double, single or absent, fugacious, prostome rare; exostome teeth well developed, less commonly rudimentary or absent, regular or irregular in shape, straight or sigmoidal, (100)213–460 x (20)60–80 µm, apices not connected, not or weakly appendiculate, papillose, striate, adaxial surface trabeculate; endostome segments well–developed, rudimentary or absent, papillose, joined at base, (10)40–450 x (22)30–113 µm; prostome rudimentary, to 10 µm

long x 24 µm wide. Spores tetrahedral, (12)25–38(55) µm, ornamentation variable: nearly smooth, verrucate–lirate, verrucate bullate, finely verrucate, smooth, weakly or lightly papillose, papillose lirate or reticulate; trilete scar usually absent, rarely present. Calyptrae cucullate, rostrate.

The genus is widely distributed, occurring in temperate, tropical and Mediterranean climates around the world, with the majority of the diversity in the Southern Hemisphere. The exact number of species in the genus is difficult to estimate because of extensive homoplasy in morphological characters across much of the family (see Chapters 2-4), but likely comprises fewer than 60 species worldwide. In Africa 12 species are recognized, with the majority of the species from subtropical and tropical areas in Southern and East Africa.

Entosthodon bergianus (Hornsch.) Müll. Hal., Syn. Musc. 1: 126. 1848. *Weissia bergiana* Hornsch., Hort. Phys. Berol. 59 (1820). *Physcomitrium bergianum* (Hornsch.) Müll. Hal., Linnaea 18: 696 (1844). *Funaria bergiana* (Hornsch.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1: 524, (1903).–TYPE: SOUTH AFRICA. Western Cape, "Montis Leonis", 15 Sept. 1816, *Bergius s.n.*(BM, holotype!).

Synonyms:

Entosthodon cavifolius Mitt., Thes. Cap. 1:64 (1859); non *Funaria cavifolia* Cardot & Broth. (1923). *Funaria harveyana* Magill, Mem. Bot. Surv. South Africa 43:7 (1979).–TYPE: SOUTH AFRICA. Western Cape, near Cape Town, *Harvey s.n.* (NY, holotype!).

Entosthodon bergii Bruch & Schimp., nom illeg., in B.S.G., Bryol. Eur. 3:256 (1841).

Entosthodon bergianus var. *minor* Rehmann, nom. nud., Bull. Misc. Inform. Kew. 1923: 203 (1923). (BOL).

Entosthodon crassipes Rehmann, nom. nud., Bull. Misc. Inform. Kew. 1923: 203 (1923). (BM).

Illustration: Figure 5.9.

Plants small, light-green. *Stems* reddish-brown, to 3 mm high, branching multiple times by sub-perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids cerise. *Leaves* erect-spreading, little contorted when dry, elliptical to oblong-obovate, 1.5–2.6 x 0.6–1.3 mm, plane to concave, short-acuminate to apiculate, entire, arista absent; *cells of upper lamina* rhomboidal to mostly oblong-hexagonal, (25)30–75 (88)

x (15) 20–33 um; *basal* (45)75–175 x (20)30–43 um; *marginal cells* undifferentiated, sometimes bulging distally near apex; *costae* ending below apex, rarely percurrent, in cross-section with two adaxial and one abaxial layer of large cells surrounding a central stereid group.

Polyoicous. *Setae* 2.5–6 (10) mm long, straight, cerise or reddish to orange-brown. *Capsules* erect or weakly inclined, radially symmetric, pyriform to oblong-pyriform, 1–1.8 x 0.5–1 mm, weakly constricted below mouth when dry, yellow to reddish-brown at maturity, with a well differentiated neck *ca.* ⅓–½ total length of capsule; *mouth* transverse, *ca.* ¾ diameter of capsule; *exothecial cells*, 28–70 x 10–20 um, in cross-section with thick, strongly cuneate anticlinal walls, 5–8 rows of oblate cells at mouth. *Opercula* plano-convex, cells not twisted. *Peristome* usually single and rudimentary, if double, endostome teeth highly reduced, to 35 um high; *exostome teeth* straight, irregular in shape, orange, tapered to an acute or rounded apex, becoming hyaline in upper ⅓, to 220 µm high, *ca.* 80 µm wide at base, striate. *Spores* 28–38 (55) µm, tetrahedral, verrucate-lirate to reticulate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Entosthodon bergianus is characterized by having leaves entire with costa ending below the apex of the leaf, upright capsules with exostome usually well developed.

Habitat and Distribution

The species is a South African winter rainfall endemic (Figure 5.8), occurring on mountain slopes of the Western and Northern Cape. It is typically found in sheltered, south-facing situations on shale derived clays, or rich humusy soils and less commonly in fynbos vegetation along the edges of small streams and com-

pact sandstone soil embankments or cutaways. *Entosthodon bergianus* is known from elevations between 300 m and 1000 m.

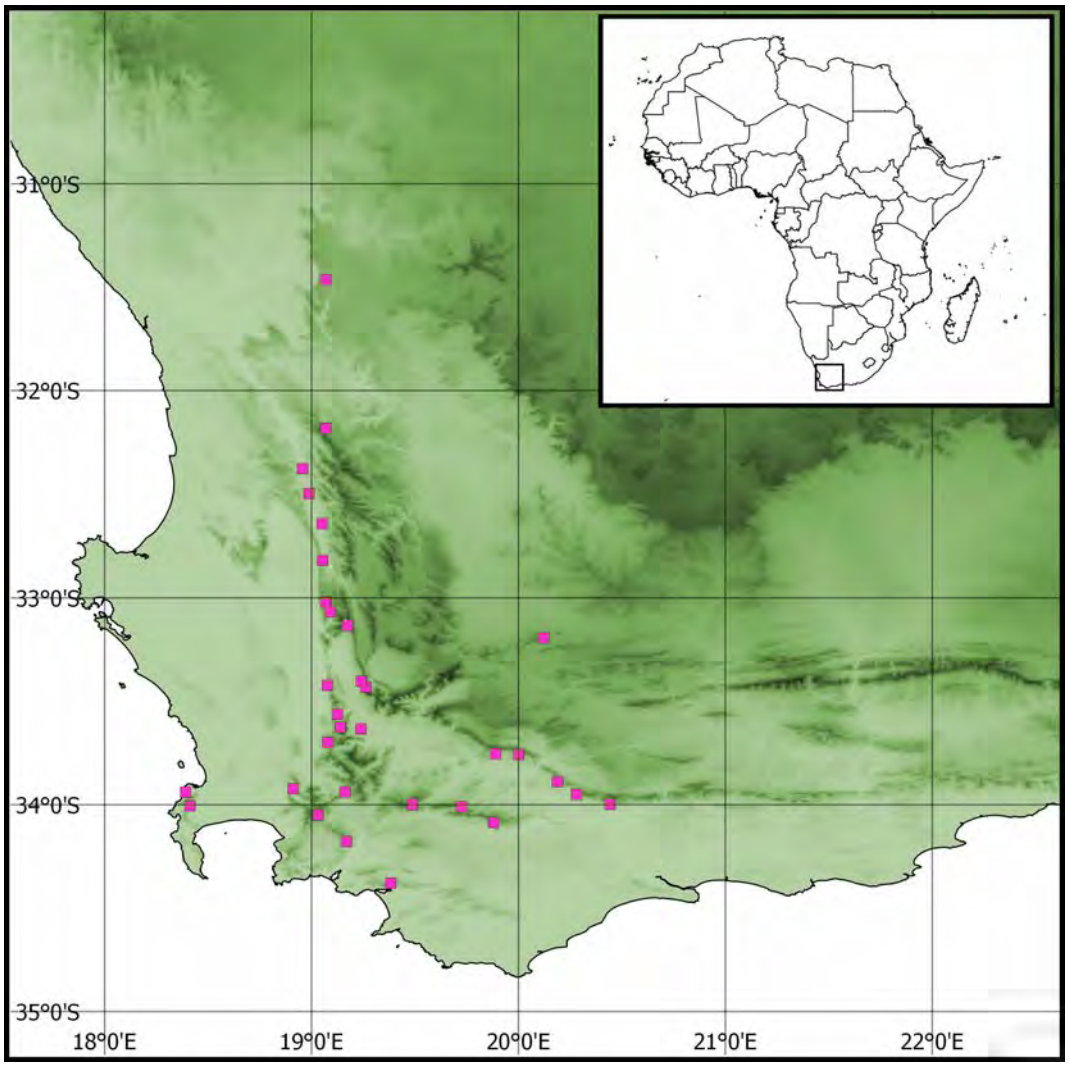

Figure 5.8: Distribution of *E. bergianus* in Africa.

Note

Entosthodon bergianus displays considerable variation in spore size. Size is usually in the range of 28–38 µm but can be as big as 55 µm although this was only observed once, consistently, in material from Bain's Kloof Pass in Wellington, South Africa.

Specimens Examined

SOUTH AFRICA. Northern Cape: Nieuwoudtville, *N. Wilding 168, 252*, 15/11/2010 (BOL); Western Cape: Ashton, *N. Wilding 225A, 225C, 225D, 225E*, 9/10/2012, *219, 229A, 229B, 229C, 229D*, 8/10/2012, 216, 6/10/2012 (BOL); Cape Town, *A. Rehmann 172*, (PRE, S: B175410), *S. Arnell 127, 290, S. Garside 6576,* (BOL, PRE), *6589* 29/8/1953 (BOL, PRE), *6607* 12/9/1953 (BOL), *6501*, 4/11/1951 (BOL), *A. Wilman CH13094*, 1/8/1957 (BOL, PRE), *Ecklon s.n.*, (E– E00477428), *N. Wilding 222*, 31/10/2012, *206, 207, 208*, 21/10/2011 (BOL); Touws River, *N. Wilding HBCT301a, HBCT301b, HBCT301c*, 5/9/2011 (BOL); Cederberg, *T.A.J. Hedderson 14381*, 6/10/2001 (BOL); Ceres–Wolsley, *T.A.J. Hedderson 16830*, 10/8/2008 (BOL); Franschoek, *N. Wilding 235,* 21/11/2012 (BOL); Groot Winterhoek, *T.A.J. Hedderson 14236, 14281, 14285, 14293, 14372*, 21/9/2001 (BOL), *N. Wilding 230, 257*, 27/10/2012 (BOL); Jonkershoek, *T.A.J. Hedderson 14136*, 7/9/2001 (BOL); Limietberg, *N. Wilding 220, 232*, 10/10/2012 (BOL); McGregor, *T.A.J. Hedderson 15250*, 28/9/2003 (BOL); Paarl, *T. Arts, RSA106/02*; *S. Garside 6607*, 26/11/1953 (BOL); Pearl Beach, *T.A.J. Hedderson 13287*, 12/8/2000 (BOL); Riversdale, *E.G.H. Oliver 7641*, 19/10/1980 (PRE); Robertson, *T.A.J. Hedderson 15564*, 7/8/2004 (BOL); Swellendam, *T.A.J. Hedderson 15276*, 11/10/2003 (PRE); *N. Wilding 228*, 6/10/2012 (BOL); Stellenbosch, *N. Wilding 236*, 21/11/2012 (BOL); Tulbagh, *N. Wilding 233A, 233B, 233C, 233D*, 2/11/2012 (BOL); Wellington, *K.H. Barnard 49632*, 1/9/1931 (PRE), *T.A.J. Hedderson 15362*, 2/11/2003 (BOL); Worcester, *E. Esterhuysen 33038*, 2/11/1972 (BOL); *E. Schelpe 7621*, 1/8/1972 (BOL), *N. Wilding 223A, 223B, 231A, 231B*, 10/10/2012 (BOL).

Figure 5.9: *Entosthodon bergianus.* 1. Habit, dry (*N. Wilding 225*, BOL); 2–4. Perichaetial leaves (2 – *N. Wilding 207*, BOL; 3 – *T.A.J. Hedderson 15564*, BOL; 4 – *N. Wilding HBCT 301a*, BOL); 5.Leaf apex (*T.A.J. Hedderson 15250*, BOL); 6. Leaf cross-section (*T.A.J. Hedderson 17741*, BOL); 7. Capsule, dry (*N. Wilding 225D*, BOL); 8. Capsule mouth & peristome (*N. Wilding 229*, BOL); 9. Operculum (*T.A.J. Hedderson 14236*, BOL); 10. Spores (*N. Wilding 168*, BOL). Scale bars: A (2–4) = 500 µm; B (5, 8) = 100 µm; C (1) = 1 mm; D (6) = 100 µm; E (10) = 50 µm; F (9) = 100 µm; G (7) = 1 mm.

Entosthodon borbonicus Besch., Ann. Sci. Nat., Bot., sér. 6, 9: 375 (1880). *Funaria borbonica* (Besch.) Broth., Nat. Pflanzenfam. [Engler & Prantl] I(3): 524 (1903).–TYPE : RÉUNION ISLAND (FRANCE), Saint–Agathe, Plaine de Palmiste, *G. De L'Isle 285* (PC lectotype!, designated here; isolectotype in BM!). I have chosen the collection from PC to serve as the lectotype because it bears the collectors name and number (*G. De L'Isle 285*), as in the protologue, while the BM specimen is recorded only as *M.G. De L'Isle s.n.*. The PC specimen is further accompanied by Bescherelle's original annotated illustrations of the species. De L'Isle 285 (PC), one of three collections listed in the protologue, is in good condition and it agrees well with Bescherelle's description of the species. The remaining two collections of De L'Isle (305 & 309) mentioned in the protologue have not been located.

Synonyms:

Funaria imerinensis Cardot, Hist. Phys. Madagascar, Mousses 270 (1915).–TYPE: MADAGASCAR. central plateau, *R.P. Villaume s.n.* (PC, holotype! (PC0134301)).

Entosthodon renauldii Thér., Suppl. Prodr. Fl. Bryol. Madagascar 53. pl. 23 f. 1 (1909).–TYPE: MADAGASCAR. central plateau, Betsileo, *R.P. Villaume s.n.* (PC, holotype! (PC0134289))

Probable synonyms:

Entosthodon hildebrandtii Müll. Hal., Flora 62: 379. 1879. *Funaria hildebrandtii* (Müll. Hal.) Broth., Bot. Jahrb. Syst. 20: 187 (1894).–TYPE: KENYA. Ndara, in Mts 2–3000 ft, *J.M. Hildebrandt s.n.* 7/2/1877. Müller's description is suggestive of *E. borbonicus*

Illustration: Figure 5.11.

Plants medium to large, light–green. *Stems* reddish–brown, to 4 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids cerise. *Leaves* erect–spreading, contorted when dry, ovate to spathulate, less frequently ovate–lanceolate, 1.5–3(3.5) x 0.5–1.3 mm, plane to slightly concave, short–acuminate, serrate in upper ½, arista absent; *cells of upper lamina* rectangular or rhomboidal to oblong–hexagonal (30)37–95 x 17–30 µm; *basal* 50–175(200) x 25–45(55) µm; *marginal cells* narrower, thicker–walled, forming a border 1–3 cells wide; *costae* ending below apex.

Polyoicous. *Setae* 5–20 mm long, straight, pale–yellow to reddish–brown. *Capsules* erect, radially symmetric, pyriform, 0.4–1.1 x 1–2 cm, constricted below mouth when dry, reddish–brown at maturity, with a well differentiated neck *ca.* ½ total length of capsule; *mouth* transverse, *ca*. ¾ diameter of capsule; *exothecial cells*, 25–60 x 10–25 (30) µm, in cross-section with thick, strongly cuneate anticlinal walls, 4–5 rows of oblate cells at mouth. *Opercula* plano–convex cells twisted anti-clockwise or not from above. *Peristome* absent. *Spores* 25–33 µm, tetrahedral, verrucate–bullate or verrucate–lirate to reticulate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Entosthodon borbonicus is characterized by its upright, radially symmetric capsules that lack a peristome and leaves that are bordered by 1–3 rows of longer, thicker–walled cells.

The leaf margins (mostly lower) can, at times, become folded across the leaf, a feature characteristic of the entire limbate complex in *Entosthodon s.s.*. The only other species treated here falling within this group is *E. limbatus*.

Habitat and Distribution

The species is typical of cool, wet habitats at *ca.* 1400–2000 m in tropical areas and much lower, *ca.* 300 m, in the extreme southerly parts of its distribution, often growing on vertical embankments and along the edges of streams. *Entosthodon borbonicus* occurs in East and southern Africa and the islands of the Western Indian Ocean and south Atlantic (Figure 5.10).

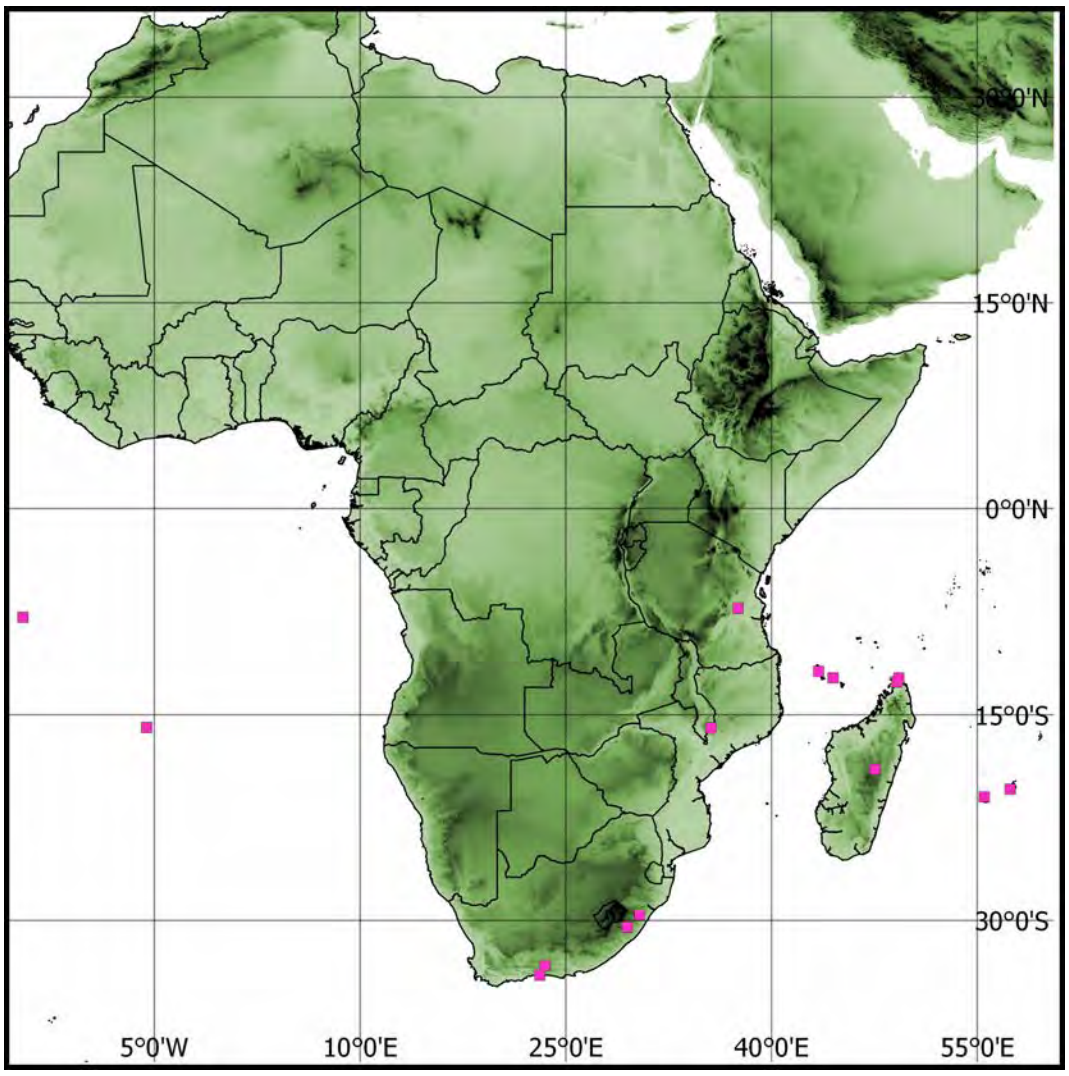

Figure 5.10: Distribution of *E. borbonicus* in Africa.

Note

Entosthodon borbonicus belongs to a widespread complex of species with, usually, limbate leaves and variable peristome states. The complex includes, among others, the African *E. limbatus*, the neotropical *E. bonplandii* and the Hawaiian endemic *E. subintegrus*. Molecular and morphology based attempts to circumscribe taxa within this complex have proven to be too big a task to complete

within the framework of this thesis. From the material that I have seen it is my opinion that the complex comprises no fewer than 5, possibly 6 different species or varieties in sub–Saharan Africa. The plasticity of the peristome characters combined with a variable leaf architecture make it difficult to intuitively interpret species boundaries; morphometric analyses or appropriate molecular data are needed to resolve this complex. I here recognize two species (*E. borbonicus* and *E. limbatus*), which are distinguished based on the presence or absence of the peristome.

Specimens Examined

ASCENSION ISLAND: Green Mountain N.P., *Ducket 11/02*, 1/2/2011 (BM).

COMOROS. Grande Comore (Ngazidja), Karthala Mt., *R.E. Magill & T. Pócs 11037*, 31/7/1992 (MO); Anjouan (Ndzouani), *R.E. Magill & T. Pócs 11271*, 11/8/1992 (MO).

MADAGASCAR. Tananarive, *R. Marshall & C.A. Crosby 9284*, 22/10/1972 (MO), *G. Kis 9468/EA*, 17/9/1994 (BOL, EGR); Diego Suarez, *R. Marshall & C.A. Crosby 7189, 7202*, 13/11/1972 (MO); Andringitra Mts., *S. Orban 9477/FL*, 24/9/1994 (BOL, EGR), *T. Pócs 9477/FO*, 24/9/1994 (BOL, EGR); Ranomafana N.P., *G. Kis 9465/DA*, 27/9/1994 (BOL, EGR); Montagne d'Ambre N.P., *P. de la Bâthie s.n.*, x/9/1926 (S: B174709).

MALAWI. Mt. Mulanje, *H. Wild 6231, 6232* (E), *T.A.J. Hedderson 17481*, 11/6/2010 (BOL).

MAURITIUS. Plaine Champagne, *G. Een M190*, 8/10/1962 (S: B8088).

RÉUNION ISLAND (FRANCE). Belouve, *G. Kis & A. Szabo 9437/CK*, 31/8/1994 (BOL, EGR), *T.A.J. Hedderson 16249*, 23/9/2006, *N. Wilding 31b*, 3/4/2010, *42*, 5/4/12010 (BOL), *J. Bardat REU1159*, 29/11/2010 (REU), *C. Ah–Peng & J. Bardat REU1380*, 28/8/2013 (BOL); La Caroline, *T.A.J. Hedderson 16301*,

28/9/2006 (BOL); Pas de Bellecombe, *N. Wilding 68*, 160 25/4/2010 (BOL); Plaine aux Sables, *C. Ah–Peng & J. Bardat REU1384*, 25/8/2013, *1382*, 23/8/2013; Piton des Neiges, *J. Bardat REU1371*, 23/8/2013, *REU1373*, 24/8/2013 (BOL); Roche Ecrit, *G. Een R401*, 11/10/1962 (S: B13304), *N. Wilding 60, 74,* 26/4/2011 (BOL); Salazie, *G. Kis 9415/CT*, *9416/CJ*, 21/8/1994 (BOL, EGR); Takamaka, *A. Szabo 9436/CR*, 30/8/1994 (BOL, EGR); Piton Lepevenche, *A. Sas–Gyarmati 9660/R*, 22/6/1996 (BOL, EGR); Piton de la Fournaise, *G. Kis & T. Pócs 9612/F*, 30/6/1996 (BOL, EGR); Langevin, *K. Pócs, T. Szabo & T. Pócs 9685/A*, 19/8/1996 (BOL, EGR).

SAINT HELENA. Diana's Peak N.P., *Wigginton 05/277A*, 28/10/2005 (Wiggington private collection; BM?); High Peak Cave, *P. Lambdon 13/001A*, 13/4/2013 (Wiggington private collection; BM?).

SOUTH AFRICA. KwaZulu–Natal: Kokstad, *J Von Breitenbach 332*, 1/10/1979 (PRE, MO); Natal, *Wager 1127* (PRE); Knoll, Zwart Kop, *Sim 10138* (PRE); Pietermaritzburg, *S.E. Wood 64*, 1/5/1973 (PRE); Mpumalanga: Buffelskloof N.R., *J. Van Rooy 4162, 4112*, 24/1/2007 (PRE, MO); Western Cape, Knysna, *S. Arnell 1551* (S:B174677); *J.P.M. Brenan 172839, 172839A*, 21/1/1971 (PRE), *N. Wilding 253*, 7/8/13 (BOL).

TANZANIA. Uluguru Mts, *R. Marshall, C.A. Crosby & T. Pócs 11317* (MO); Usambara, *Holst 1089* (S: B175354).

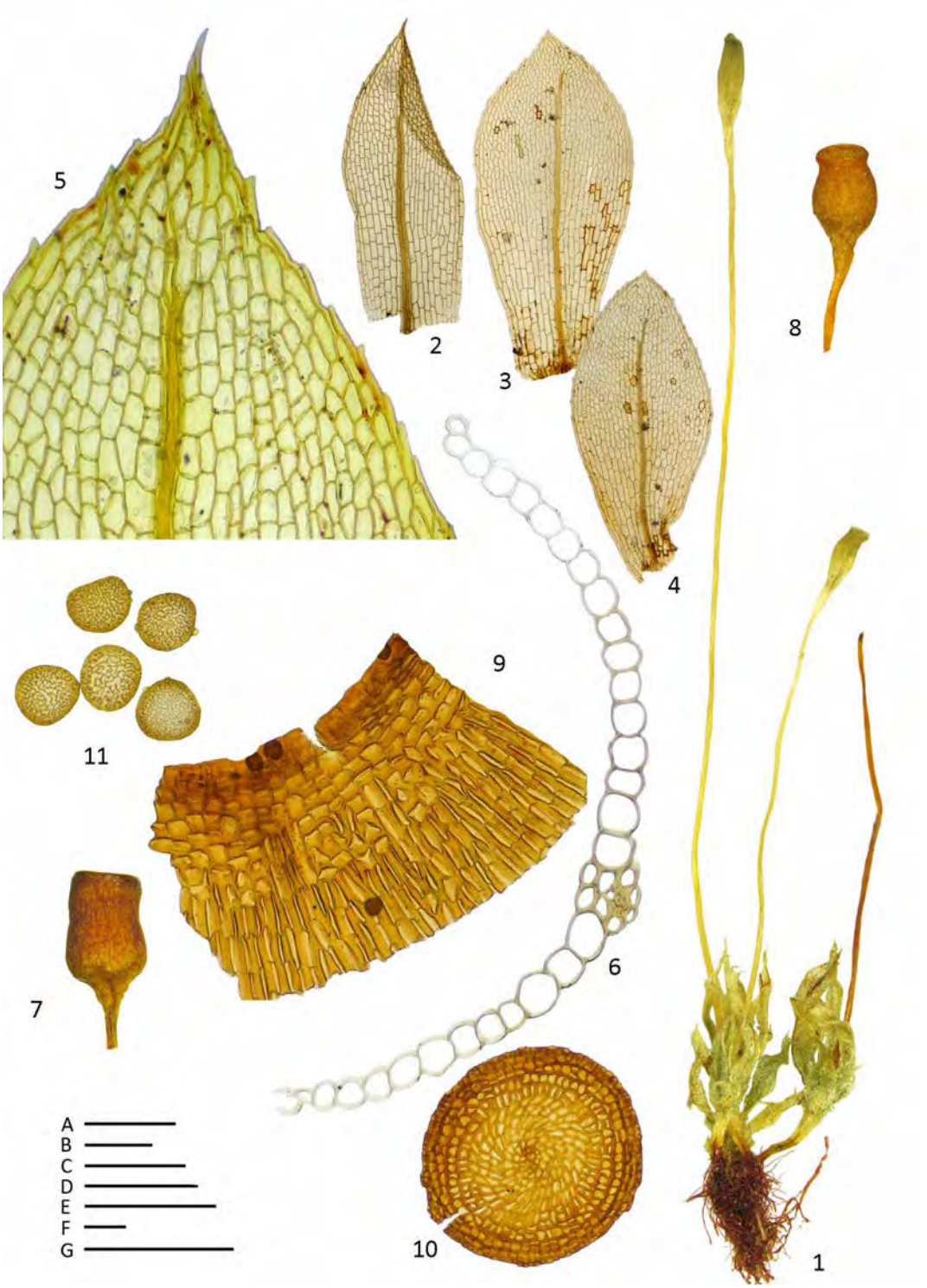

Figure 5.11: *Entosthodon borbonicus.* 1. Habit, dry (*T.A.J. Hedderson 16249*, BOL); 2–4. Leaves (2 – *R.E. Magill & T. Pócs 11037*, MO; 3, 4 – *N. Wilding 172*, BOL); 5. Leaf apex (*G. De L'Isle 285*, PC); 6. Leaf cross-section (*T.A.J. Hedderson 17481*, BOL); 7–8. Capsule, dry (as for 1); 9. Capsule mouth & exothecial cells (as for 1); 10. Operculum (*R. Marshall, C.A. Crosby & T. Pócs 11317*, MO); 11. Spores (*J. Bardat REU1159*, REU). Scale bars: A (2–4) = 500 µm; B (5, 9) = 100 µm; C (1) = 1 mm; D (6) = 100 µm; E (11) = 50 µm; F (10) = 100 µm ; G (7, 8) = 1 mm.

Entosthodon cameruniae (Dixon) N. Wilding *comb. nov.* Basionym: *Funaria cameruniae* Dixon, Ann. Bryol. 6: 23 (1933).–TYPE: CAMEROON. Mt. Cameroon, slopes near Hut II, 10,000 ft, *M. Steele 42*, 11/1/1932 (BM, holotype!).

Illustration: Figure 5.13

Plants medium, light-green. *Stems* reddish-brown or cerise, to 5 mm high, branching multiple times by sub-perigonial innovation, in cross section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids cerise. *Leaves* erect-spreading, contorted when dry, oblong-obovate to ovate-lanceolate, (1.3)1.6–2.6 x 0.5–0.8(1) mm, concave, short-acuminate, entire to weakly serrate in upper ⅓, aristate, arista, if present, to 300 µm; *cells of upper lamina* quadrate to oblong hexagonal, 35–63(75) x 17–30(35) µm; *basal* (90)100–200(225) x 22–40(63) µm; *marginal cells* narrower, thicker-walled, sometimes forming a border 1–2 cells wide; *costae* ending below apex.

Polyoicous. *Setae* (3)8–15(20) mm long, straight to arcuate, pale-yellow to reddish-brown. *Capsules* erect to horizontal, gibbous, zygomorphic to almost radially symmetric, oblong-obovoid, 1.4–2.5 x 0.4–0.9 mm, constricted below mouth when dry, reddish–brown at maturity, with a well differentiated neck *ca.* ½ total length of capsule; *mouth* slightly oblique to transverse, *ca.* ¾ diameter of capsule; *exothecial cells*, 45–80 x 10–18 µm, in cross-section with thick, strongly cuneate anticlinal walls, 3–5 rows of oblate cells at mouth. *Operculum* plano–convex, cells not or slightly twisted anti-clockwise from above. *Peristome* double; *exostome teeth* straight, regular in shape, orange, tapered to an acute apex, becoming hyaline in upper ⅓, to 213 µm high, *ca.* 50 µm wide at base, striate, trabeculate; *endostome teeth* rudimentary, hyaline, to 30 µm high and 78 µm

wide. *Spores* 25–38 µm, tetrahedral, verrucate-lirate to reticulate, rarely bullate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Entosthodon cameruniae can be distinguished by its oblong-obovate to ovate-lanceolate leaves, zygomorphic, gibbous capsules with rudimentary endostome and verrucate-lirate to reticulate spores.

Habitat and Distribution

The species is known from Cameroon and Ethiopia (Figure 5.12) at elevations between 2100 m and 3050 m. *Entosthodon cameruniae* has been collected in basalt crevices in grassland along seepages and vertical faces of peaty humus encrusted with liverworts and other mosses.

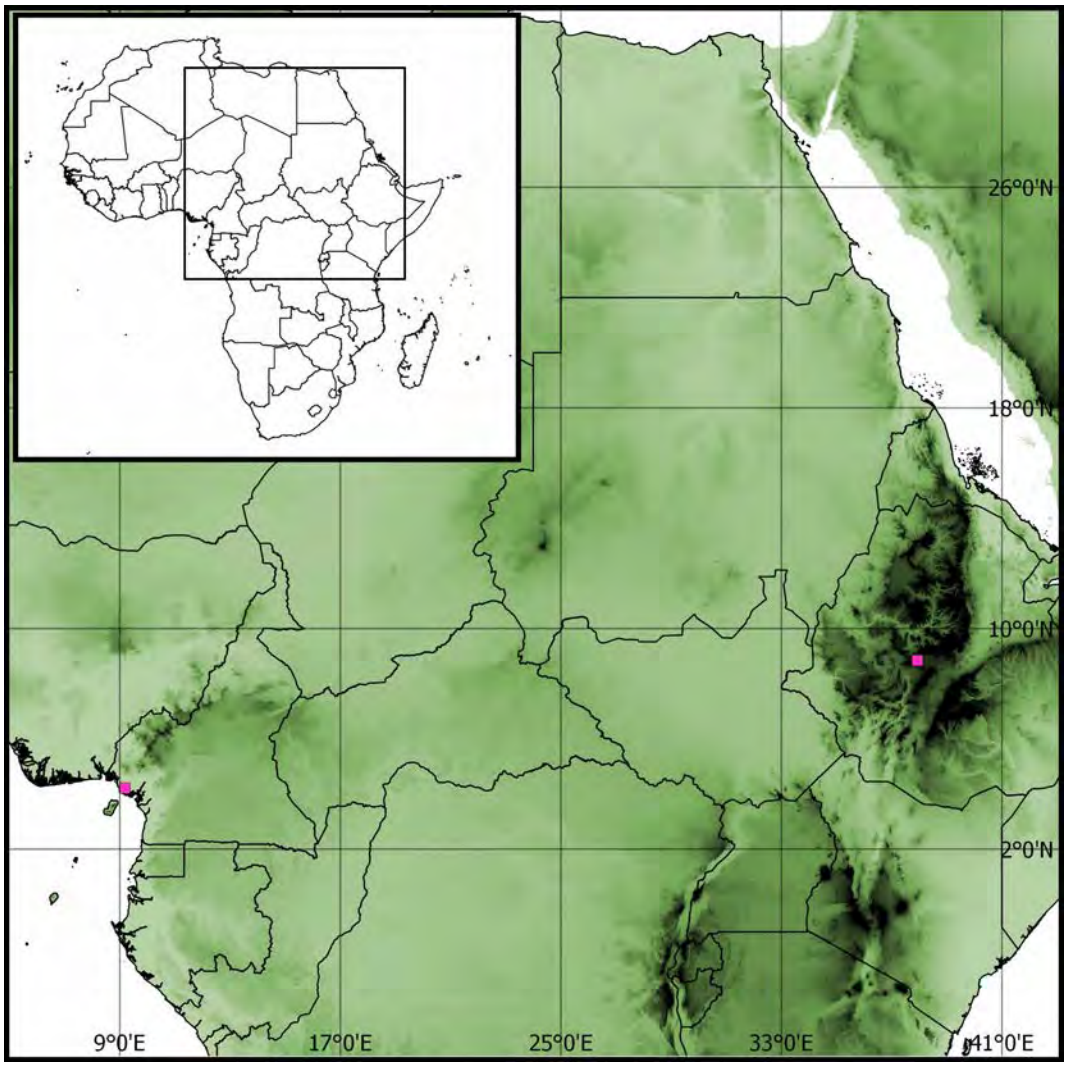

Figure 5.12: Distribution of *E. cameruniae* in Africa.

Note

Entosthodon cameruniae may be confused with *E. curvipes*, which according to Mitten (1863) is also present on Mt. Cameroon between 2100 m and 2700 m, however, the former differs in having a rudimentary endostome, smaller, less strongly bordered oblong-obovate to ovate-lanceolate leaves.

Note 2

An almost full spectrum of capsule shapes has been observed in the few collections from Mt. Cameroon from erect, almost radially symmetric to horizontal, gibbous and zygomorphic.

Specimens Examined

CAMEROON. Cameroon Mountain, *E.W. Jones in P.W. Richards 4148* 24–29/3/1948, *4232* 27/3/1948, *4343* 1/4/1948(MO), *J.P.M. Brenan in P.W. Richards 4183* 26/3/1948 (MO).

ETHIOPIA. Gojam, *D.A Petelin 25–2*, 13/12/1990 (MO).

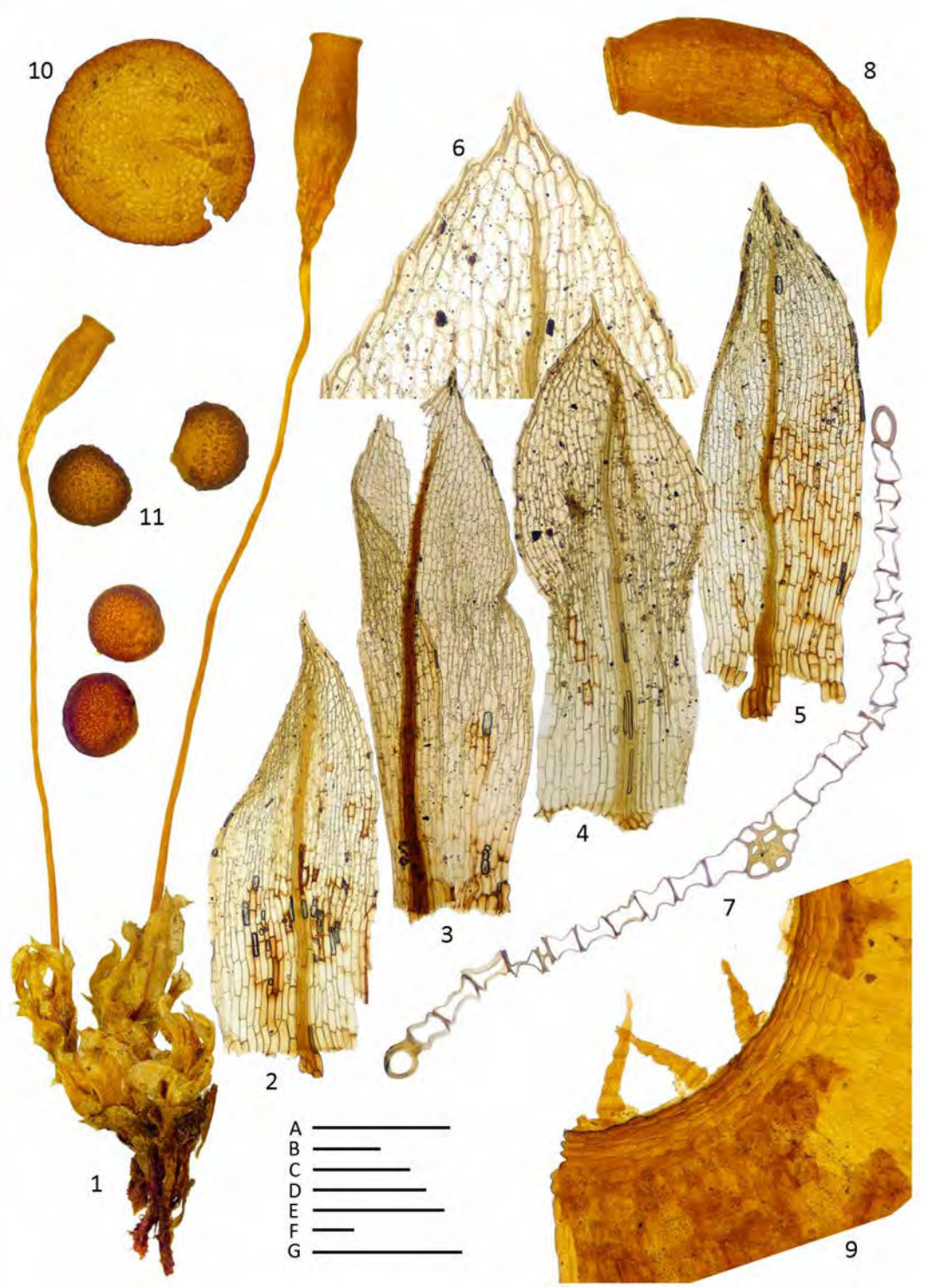

Figure 5.13: *Entosthodon cameruniae.* 1. Habit, dry (*J.P.M. Brenan in P.W. Richards 4183*, MO); 2–5. Leaves (2–5 – as for 1); 4 – *E.W. Jones in P.W. Richards 4232*, MO); 6. Leaf apex (as for 1); 7. Leaf cross-section (*E.W. Jones in P.W. Richards 4343*, MO); 8. Capsule, dry (as for 7); 9. Capsule mouth & peristome (*M. Steele 42*, BM); 10. Operculum (as for 9); 11. Spores (as for 9). Scale bars: A (2–5) = 500 µm; B (6, 9) = 100 µm; C (1) = 1 mm; D (7) = 100 µm; E (11) = 50 µm; F (10) = 100 µm; G (8) = 1 mm.

Entosthodon claudineae N. Wilding sp. nov.–TYPE: TANZANIA. Mt. Meru, Engare Narok Gorge. 3400–3500 m. *T. Pócs, R. Ochyra & H. Bednarek–Ochyra, 88152/BH* (BOL, holotype!; isotype in EGR!).

The species is named in honour of my wife and fellow bryologist, Claudine Ah-Peng.

Illustration: Figure 5.15.

Plants small, light–green. *Stems* reddish–brown, to 4 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids cerise. *Leaves* erect–spreading, little contorted when dry, ovate–lanceolate to obovate, 1.5–2.1 x (0.5)0.7–1.4 mm, concave, short acuminate to apiculate, entire to weakly serrate in upper ⅓, in some populations forming an arista to 270 µm; *cells of upper lamina* quadrate to hexagonal, (27)40–58(73) x (17)25–35(40) µm; *basal* (60)85–125(163) x 22–35(43) µm; *marginal cells* often forming weak border of narrower cells, one cell wide, in upper ½; *costae* ending below the apex.

Polyoicous. *Setae* 6–12 mm long, curved, flexuose, reddish–brown. *Capsules* inclined to horizontal, gibbous, zygomorphic, oblong-pyriform 2–2.6 x 0.7–0.9 mm, weakly constricted below mouth when dry, reddish–brown at maturity, with a well differentiated neck *ca.* ½ total length of capsule; *mouth* transverse, *ca.* ⅔ diameter of capsule; *exothecial cells*, (37)45–70(85) x 12–18(23) µm, in cross-section with thick, strongly cuneate anticlinal walls, 4–5 rows of oblate cells at mouth. *Opercula* plano–convex, cells not or slightly twisted anti–clockwise from above. *Peristome* double, rudimentary prostome to 10 µm high 8 µm wide; *exostome teeth* straight to weakly sigmoidal, regular in shape, orange, tapered to acute apices, often becoming hyaline in upper ⅓, to 225 µm high, *ca.* 63 µm wide at

base, smooth to strongly papillose with papillae to 2.5 µm high, and/or striate, trabeculate, weakly appendiculate; *endostome teeth* smooth to finely papillose, hyaline, to 70 µm high and 75 µm wide. *Spores* 30–38(43) µm, tetrahedral, verrucate–lirate to reticulate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Among the African species *E. claudineae* is recognizable by the combination of mucronate/aristate leaves that are often bordered or weakly toothed in the upper third, zygomorphic capsules with often strongly ornamented (see description) peristome teeth and a rudimentary prostome.

Habitat and Distribution

The species is known from one population in central Ethiopia and two populations in northern Tanzania (Figure 5.14). The species occurs on high mountain slopes *ca.* 2900–3500 m in herbaceous afro–alpine grassland.

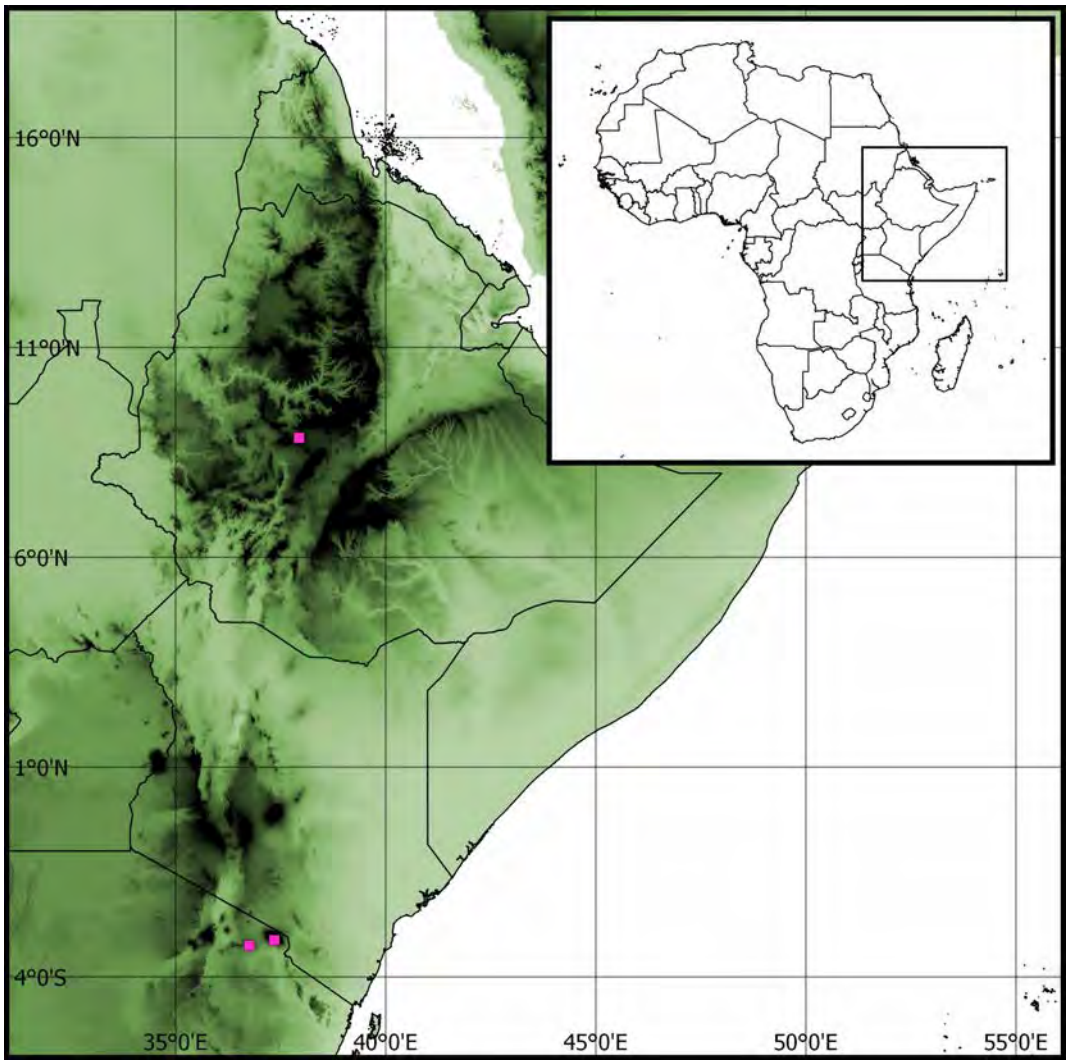

Figure 5.14: Distribution of *E. claudineae* in Africa.

Specimens Examined

ETHIOPIA. Shewa, *D.A. Petelin 11–2*, 14/10/1990 (MO).

TANZANIA. Arusha N.P.,*T. Pócs & Helsinki Univ. Bot. Dept. 88094/BH, 88093/D*, 26/5/1988 (BOL, EGR), *T. Pócs, D. Harrison & J.M. Mushy 90130/UV,* 9/6/1990 (BOL, EGR), *T. Pócs & J. Linden 90030/S, 90033/G,* 17/2/1990 (BOL, EGR); Kilimanjaro Mts., *T & A . Pócs & B.O. van Zanten 86132/A*, 9/8/1968 (EGR);

Mt. Meru, T. Pócs, G. Kabuta & J. Makunka 8685/OPQ, 14/6/1986 (BOL, EGR), *T. Pócs, E. Frater & G. Kosa 87169/AL*, 18/6/1987 (BOL, EGR).

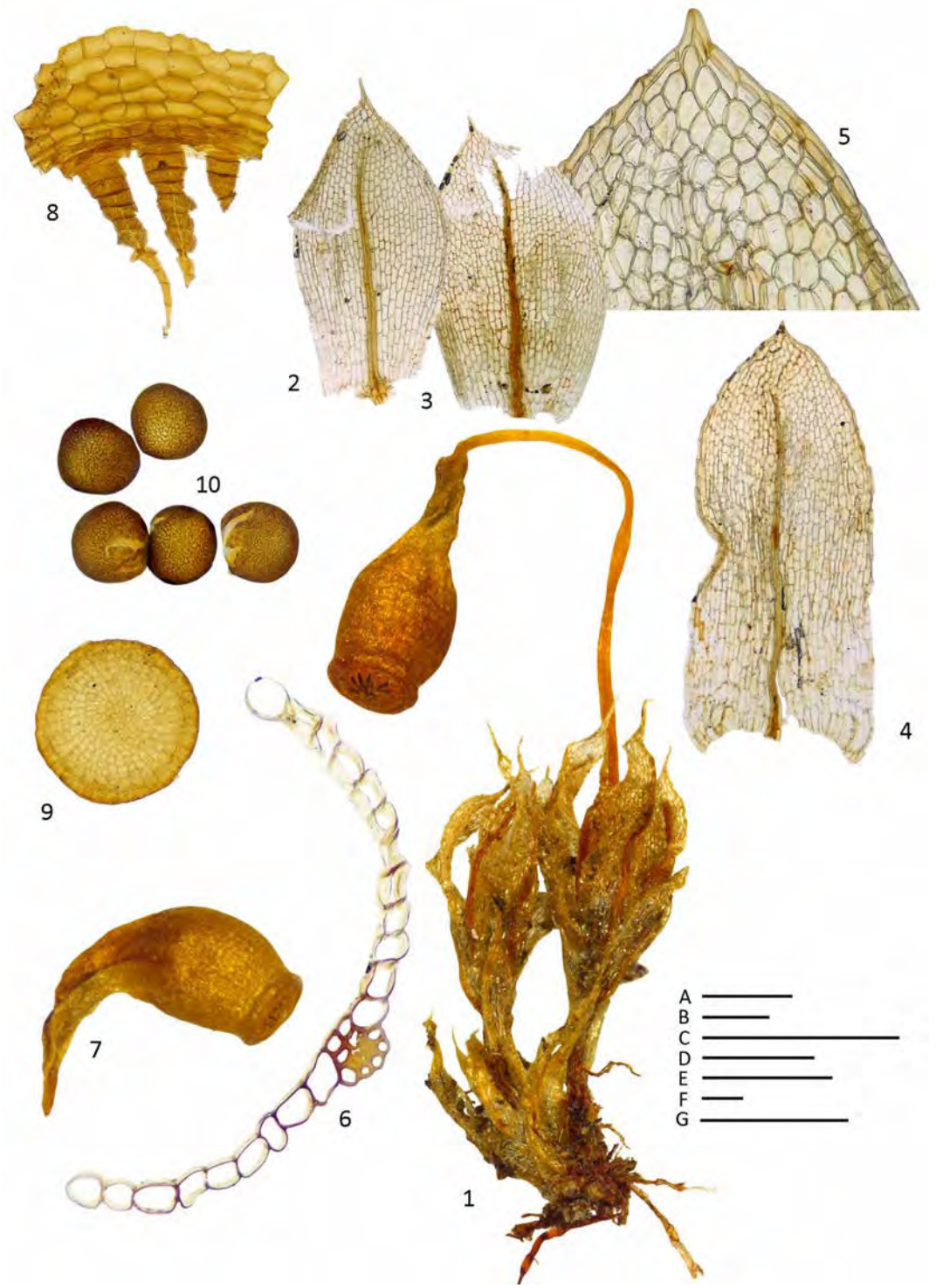

Figure 5.15: *Entosthodon claudineae.* 1. Habit, dry (*T. Pócs, G. Kabuta & J. Makunka 8685/OPQ*, BOL, EGR); 2–4. Leaves (2, 3 – *T. Pócs & Helsinki Univ. Bot. Dept. 88094/BH*, BOL, EGR; 4 – *T. Pócs, E. Frater & G. Kosa 87169/AL*, BOL, EGR); 5. Leaf apex (as for 4); 6. Leaf cross-section (as for 1); 7. Capsule, dry (as for 1); 8. Capsule mouth & peristome (*T. Pócs, R. Ochyra & H. Bednarek–Ochyra, 88152/BH*, BOL, EGR); 9. Operculum (as for 1); 10. Spores (*T. & A . Pócs & B.O. van Zanten 86132/A*, EGR). Scale bars: A (2–4) = 500 µm; B (5, 8) = 100 µm; C (1) = 1 mm; D (6) = 100 µm; E (10) = 50 µm; F (9) = 100 µm; G (7) = 1 mm.

Entosthodon curvipes (Müll. Hal.) Müll. Hal., Syn. Musc. Frond. 1: 123 (1848). Physcomitrium curvipes Müll. Hal., Linnaea 18: 697 (1844[1845]).–TYPE: TANZANIA. Mt. Meru, SW slope of summit area, 3300–3400 m, *T. Pócs 8687/AB*, 15/6/1986 (BOL, neotype!, designated here; isoneotype in EGR!, SUA!). The original type collection, Schimper's no. 1393, appears in NYBG under *Didymodon abyssinicus* Schimp. and at Kew under *Hypericum quartinianum* A.Rich. and possibly others. From this I gather that Schimper's no. 1393 was a fairly large collection of material that was likely separated into what he perceived as different species and from there forwarded to different authorities. Since searches of multiple herbaria with large collections of Schimper's duplicates have turned up nothing, I assume Müller probably received the only packet containing material of *E. curvipes* and I believe this to have been destroyed during the Allied bombing of Germany in WWII. Thus I have chosen material which I believe best conforms to Müller's *E. curvipes* to serve as the neotype.

Synonyms:

Entosthodon curvipes var. robustior Müll. Hal., Syn. Musc. Frond. 1: 123 (1848).–TYPE: ETHIOPIA. Locality, collector and date unknown. No specimen found.

Entosthodon volkensii (Broth.) Paris, Index Bryol. Suppl. 142 (1900). *Funaria volkensii* Broth., Bot. Jahrb. Syst., 24: 243 (1897).–TYPE: TANZANIA. Kilimanjaro, 3200 m, *Volkens 1225* (S, lectotype!, designated here.). No specimen was found in H which houses Brotherus's herbarium. For this reason, and because it is the only specimen of *Volkens 1225* known, I have chosen the specimen from S to serve as the lectotype.

Funaria perlaxa Thér., Rev. Bryol., 3: 34. 3 (1930).–TYPE: DEMOCRATIC REPUBLIC OF THE CONGO. Mt. Mikeno, Camp Rueru, 3120 m, *D.H. Linder 2330*, x/3/1920 (HUH, holotype!).

Funaria radians Bruch *et* Schimp., nom. inval., Syn. Musc. Frond. 1: 122. (1846) (BOL).

Illustration: Figure 5.17.

Plants medium, light–green. *Stems* to 4 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1-2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids cerise. *Leaves* erect–spreading, contorted when dry, elliptical to spathulate, 2–3.8 x 0.7–2.3 (2.7) mm, concave, short acuminate, entire to weakly serrate in upper ⅔, arista absent; *cells of upper lamina* quadrate to hexagonal or oblong hexagonal, 37–85 (113) x 27–38 µm; *basal* (75) 95–200 x 30–55 (68) µm; *marginal cells* narrower, thicker-walled, forming a border 1–2 cells wide; *costae* ending below apex.

Polyoicous. *Setae* 4–11(20) mm long, straight to curved, pale–yellow to reddish–brown. *Capsules* inclined to horizontal, gibbous, zygomorphic, pyriform to oblong-pyriform, 2–2.5 x 0.9–1.2 mm, often weakly constricted below mouth when dry, reddish–brown at maturity, with a well differentiated neck *ca*. ½ total length of capsule; *mouth* slightly oblique, *ca*. ¾ diameter (equal diameter in older dry capsules) of capsule; *exothecial cells* 30–55 x 10–25 µm, in cross-section with highly thickened, remarkably strongly cuneate anticlinal walls, 4–8 rows of oblate cells at mouth. Opercula short–conic, cells twisted anti–clockwise from above. *Peristome* double; *exostome teeth* straight to sigmoidal, regular in shape, orange, tapered to an acute or rounded apex, to 460 µm high, *ca*. 95 µm wide at base, smooth to papillose (papillae more prominent near apices), striate, trabeculate; *endostome teeth* straight to sigmoidal, smooth to weakly papillose, striate, pale–yellow, to 450 µm high and 113 µm wide at base. *Spores* 25–35 µm, tetrahedral, finely verrucate–lirate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

The entire to weakly serrate, bordered leaves, zygomorphic, gibbous capsules and finely verrucate–lirate spores set it apart from other African species. The strongly thickened exothecial cells which are usually present are characteristic of *E. curvipes* and make the species easy to identify.

Habitat and Distribution

Entosthodon curvipes is known from the high mountains of Ethiopia, Kenya, Rwanda and Tanzania (Figure 5.16). It has been collected in Ericaceous vegetation at elevations between 1320 m and 4800 m. According to Mitten (1863) the species is present on Mt. Cameroon between 2100 m and 2700 m and the material agrees exactly with Ethiopian material; I have not seen this material.

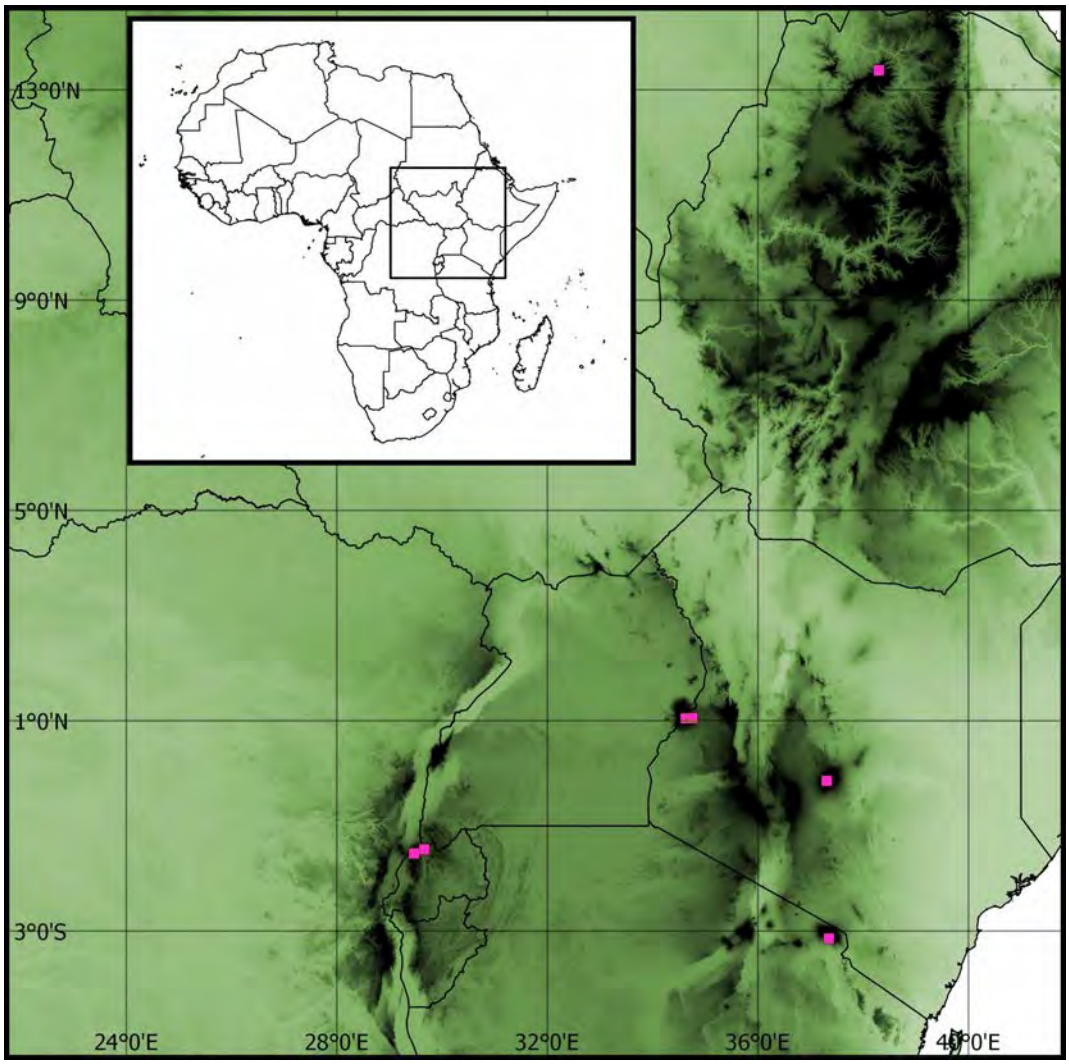

Figure 5.16: Distribution of *E. curvipes* in Africa.

Note

Entosthodon curvipes can be confused with *E. zygolimbatus* as both species can have limbate leaves and peristomate, zygomorphic capsules. The former differs, however, by having less strongly dentate, limbate leaves and spores that are finely verrucate–lirate. Can also be confused with *E. cameruniae* (see Note under *E. cameruniae*).

Specimens Examined

TANZANIA. Tanganyika Territory Mt. Meru, *O. Hedberg 2418* (S: B174579), *T. Pócs, R. Ochyra & H. Bednarek–Ochyra 88152/W*, 24/6/1988 (BOL, EGR); Kilimanjaro Mts., *T & A . Pócs & B.O. van Zanten 86136/A*, 11/8/1986 (G, EGR, MO), *86131/R*, 8/8/1986 (EGR, MO), *86131/X*, 8–11/8/1986 (EGR, MO), *A.J. & Evelyn Sharp et al. 43/A*, 11/7/1968; *T. Pócs 6719/A*, 29/6/1972 (EGR).

KENYA. Mt Elgon, *O. Hedberg 235* (S:B175351), *C.C. Townsend 77/146* (MO), *T. Pócs & A. Szabo 9218/DN*, 15/1/1992 (EGR), *T. Pócs, M.S. Chuah, E.M. Kungu & students 9212/S*, 11/1/1992 (EGR); Mt. Kenya, *J. Spence 2655a*, 26/6/1984 (EGR), *S. Rojkowski 147*, 31/12/1975 (EGR), *Dummer–Maclennan 2391B, 3414B*, 1/1918 (EGR).

RWANDA. Muhavura Mts, *W.G. D' Arcy 9041* (MO); Visoke–Karisimbe saddle, *W.G. D' Arcy 7624*, 7/2/1975 (EGR); Karisimbi, *T. Pócs 8081*, 14/9/1991 (EGR).

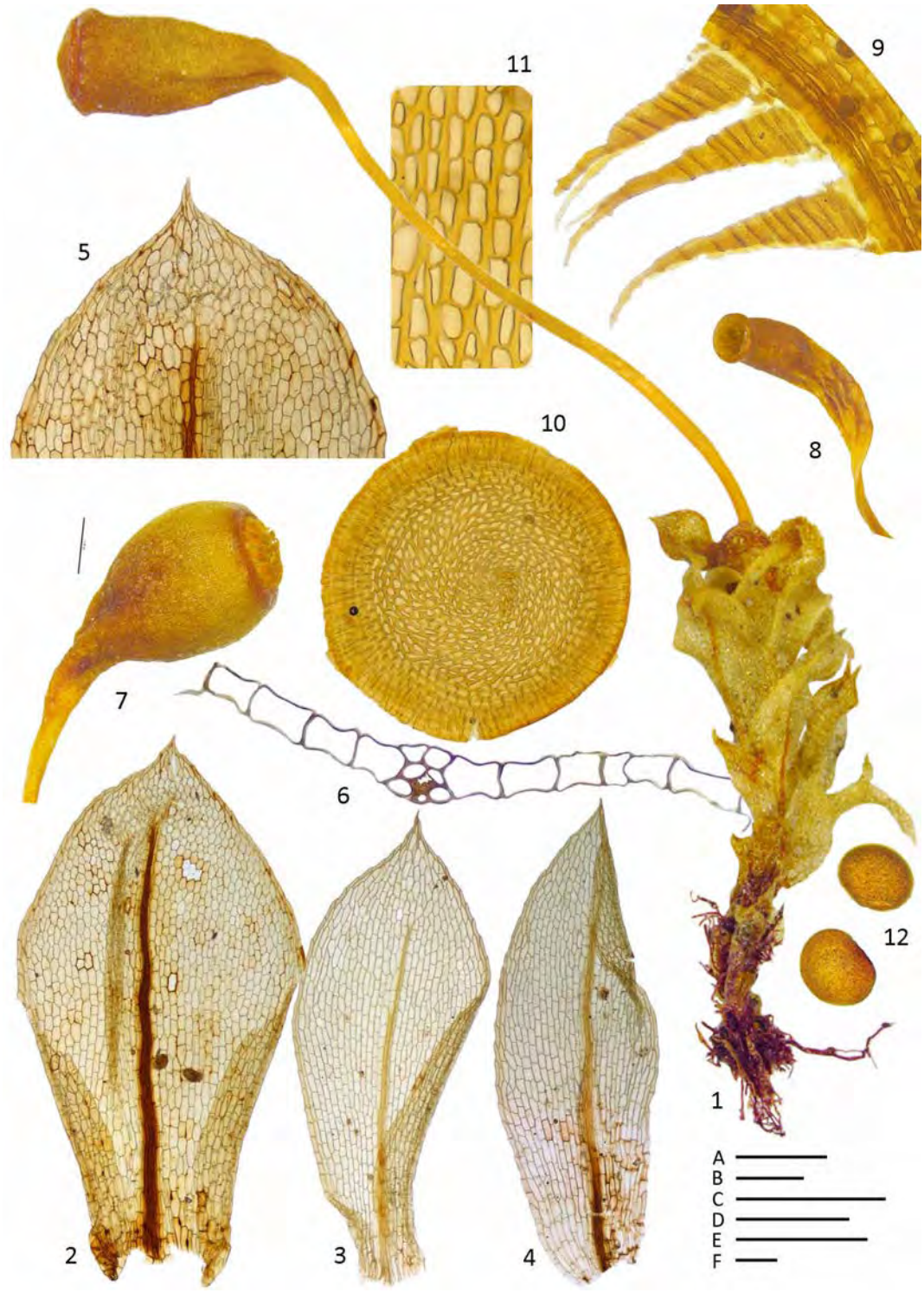

Figure 5.17: *Entosthodon curvipes*. 1. Habit, dry (*T. Pócs & A. Szabo 9218/DN*, EGR); 2–4. Leaves (*2 – T. Pócs, R. Ochyra & H. Bednarek–Ochyra 88152/W*, EGR; 3, 4 – *T & A . Pócs & B.O. van Zanten 86136/A*, EGR); 5. Leaf apex (as for 2); 6. Leaf cross-section (*T. Pócs 8687/AB*, EGR); 7, 8. Capsule, dry (7 – as for 1; 8 – *T. Pócs, M.S. Chuah, E.M. Kungu & students 9212/S*, EGR); 9. Capsule mouth & peristome (as for 2); 10. Operculum (*T. Pócs 6719/A*, EGR); 11. Exothecial cells (as for 10); 12. Spores (as for 6). Scale bars: A (2–4) = 500 µm; B (5, 9) = 100 µm; C (1, 7, 8) = 1 mm; D (6, 11) = 100 µm; E (12) = 50 µm; F (10) = 100 µm.

Entosthodon heddersonii N. Wilding sp. nov.–TYPE: TANZANIA. S–Uluguru Mts. E–edge of Lukwangule Plateau, 2350–2370 m. *T. Pócs, R. Ochyra & H. Bednarek–Ochyra 88108/V* (BOL, holotype!; isotype in EGR!).

This species is named in honour of my mentor, Terry A.J. Hedderson, for his work on the group and his passion for African bryology.

Illustration: Figure 5.19.

Plants small, light–green. *Stems* reddish–brown, to 3 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids cerise. *Leaves* erect–spreading, contorted when dry, narrowly oblong–obovate, (0.75)1.2–1.6(1.9) x 0.4–0.6 mm, plane to slightly recurved, short acuminate, serrate in upper ⅔, aristate, arista to 300 µm; *cells of upper lamina* quadrate to oblong hexagonal, 37–63 x 15–25 µm; *basal* 50–125 x 20–30 µm; *marginal cells* longer and narrower, thicker–walled, forming a border one cell wide; *costae* ending below apex.

Polyoicous. *Setae* 5–13 mm long, straight to curved, pale–yellow to reddish–brown. *Capsules* inclined to horizontal, gibbous, zygomorphic, oblong-obovoid, 1.4–2.5 x 0.5–1 mm, weakly constricted below the mouth when dry, yellow to reddish–brown at maturity, with a well differentiated neck *ca*. ½ the total length of the capsule; *mouth* slightly oblique, *ca*. ¾ the diameter of the capsule; *exothecial cells* 15–25 x 3–7 µm, in cross-section with thick, strongly cuneate anticlinal walls, 3–5 rows of oblate cells at mouth. *Opercula* plano–convex, cells twisted anti–clockwise from above. *Peristome* double; *exostome teeth* straight, regular in shape, orange, tapered to an acute apex, to 100 µm high, *ca*. 20 µm wide at base, smooth, striate, trabeculate; *endostome teeth* smooth, hyaline, to 40 µm high and 30 µm wide. *Spores* 30–35 µm, tetrahedral, verrucate–lirate to reticulate. *Calyp-*

trae cucullate, rostrate.

Diagnostic Features

Entosthodon heddersonii is easily recognized by its narrowly oblong–obovate, aristate leaves, which are bordered and toothed in the upper ⅔.

Habitat and Distribution

The species is known only from the type collection in the Uluguru Mountains of Tanzania (Figure 5.18). The type of *E. heddersonii* was collected at *ca*. 2360 m along a rocky, peaty stream bank on the eastern edge of the Lukwangule Plateau.

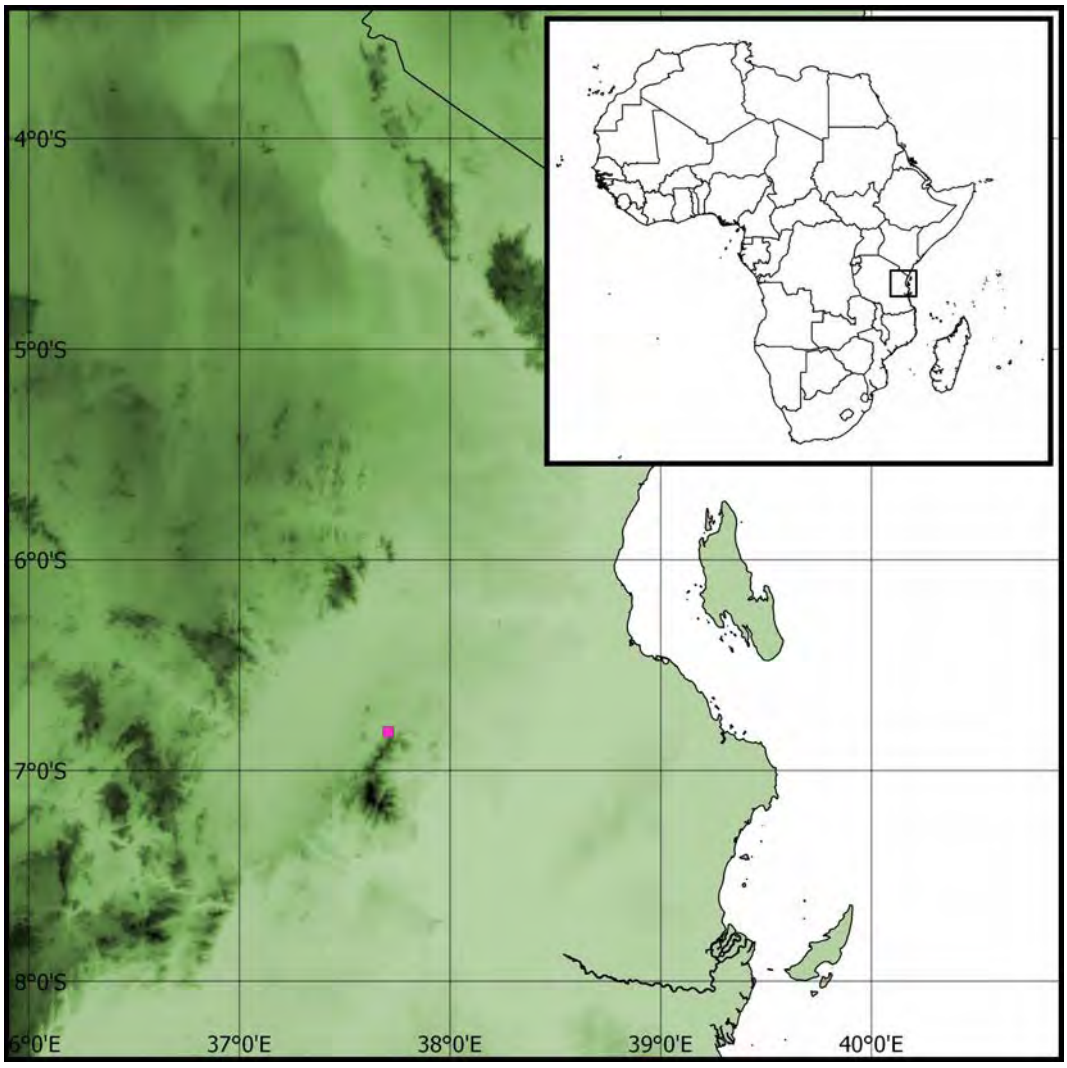

Figure 5.18: Distribution of *E. heddersonii* in Africa.

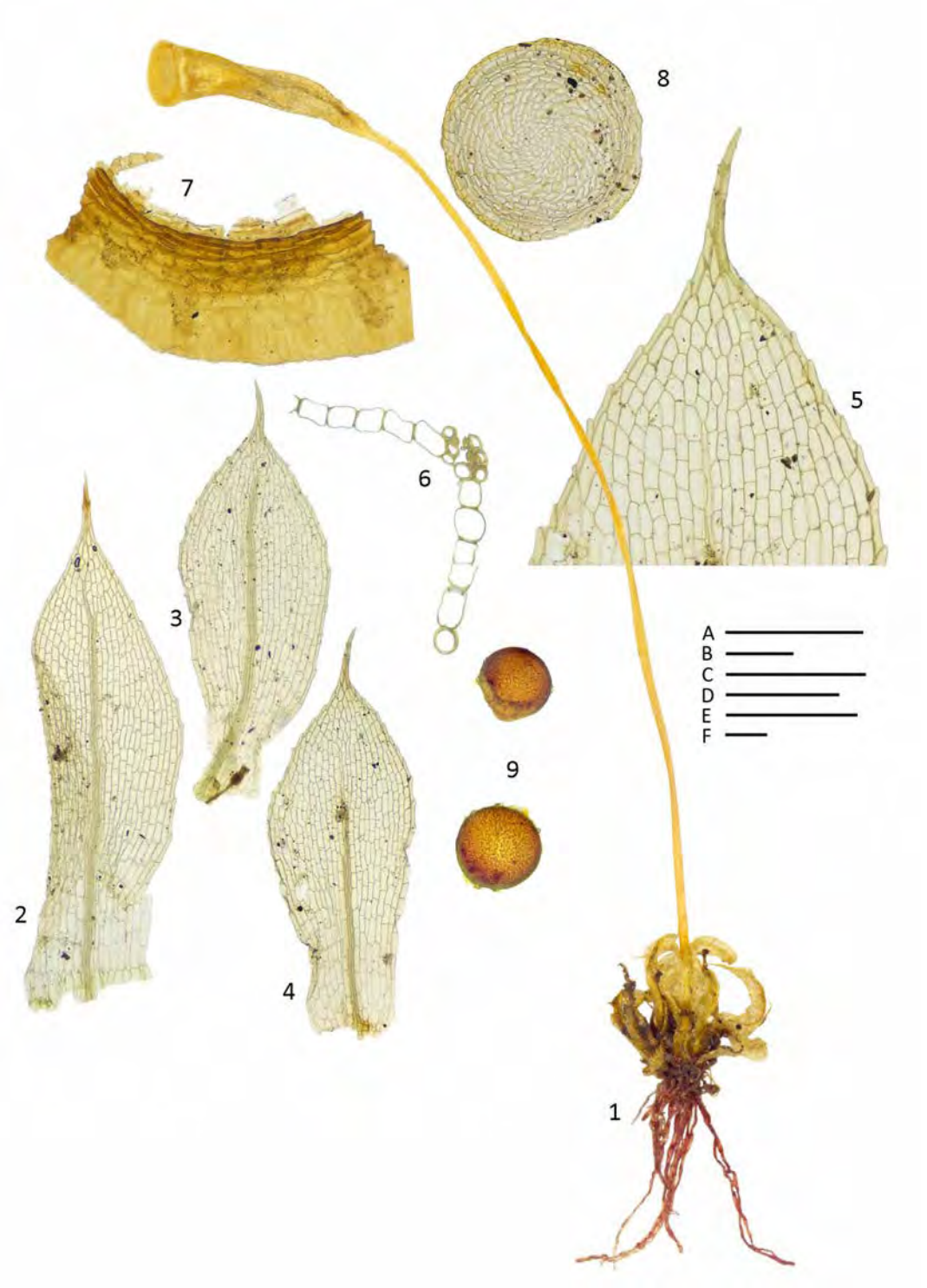

Figure 5.19: *Entosthodon heddersonii.* 1. Habit, dry; 2–4. Leaves; 5. Leaf apex; 6. Leaf cross-section; 7. Capsule mouth & peristome; 8. Operculum; 9. Spores. All from — *T. Pócs, R. Ochyra & H. Bednarek–Ochyra 88108/V*, BOL. Scale bars: A (2–4) = 500 µm; B (5, 7) = 100 µm; C (1) = 1 mm; D (6) = 100 µm; E (9) = 50 µm; F (8) = 100 µm.

Entosthodon lepervanchei Besch., Ann. Sci. Nat., Bot., sér. 6, 9: 375 (1880).–TYPE: RÉUNION ISLAND (FRANCE). *P. Lepervanche s.n.* (PC, lectotype!, designated here; isolectotype in BM!). Despite the location of Bescherelle's exotic material in BM, I have chosen the PC specimen to serve as the lectotype. I believe that the PC specimen was also seen by Bescherelle as it is accompanied by illustrations in his own hand.

Illustration: Figure 5.21.

Plants medium, light–green. *Stems* reddish–brown, to 5 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids cerise. *Leaves* erect–spreading, contorted when dry, ovate to oblong obovate, 2.2–3.4 x 0.8–1.4 mm, plane to slightly concave, short-acuminate to acuminate, entire, arista absent; *cells of upper lamina* quadrate to oblong–hexagonal, 47–70(88) x 25–38(45) µm; *basal* (105)137–238(275) x 27–45(53) µm; *marginal cells* narrower, thicker–walled, forming a border 1–3 cells wide; *costae* ending below apex.

Polyoicous. *Setae* (15)20–30(40) mm long, straight, pale–yellow to reddish–brown. *Capsules* inclined to horizontal, gibbous, zygomorphic, oblong-obovoid, 2.5–4 x 0.7–1.2 mm, constricted below mouth when dry, yellowish–green to reddish–brown at maturity, with a well differentiated neck *ca.* ½ total length of capsule; *mouth* transverse, *ca*. ¾ to equal diameter of capsule; *exothecial cells*, (35)50–75(88) x 12–23(28) µm, in cross-section with thick, strongly cuneate anticlinal walls, 4–6 rows of oblate cells at mouth. *Opercula* plano–convex, cells twisted anti–clockwise from above. *Peristome* double, rudimentary prostome often visible; *exostome teeth* straight to weakly sigmoidal, regular in shape, reddish–orange, tapered to

an acute apex, to 160 µm high, *ca*. 30 µm wide at base, papillose, weakly papillose, striate, trabeculate, weakly appendiculate; *endostome teeth* rudimentary, smooth to finely papillose, pale-yellow, hyaline, to 15 µm high and 30 µm wide. *Spores* 27–35 µm, tetrahedral, finely to coarsely verrucate–lirate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Entosthodon lepervanchei is a distinctive species, easily recognized by its bordered leaves, unusually long seta, zygomorphic capsules with well developed endostome and rudimentary prostome.

Habitat and Distribution

The species is thus far known only from Réunion Island (Figure 5.20) where it occurs on humusy substrates, e.g. along south facing cliff faces or on thin layers of soil/humus covering rocks in shaded situations. *Entosthodon lepervanchei* has been recorded from elevations between 2200 m and 2500 m.

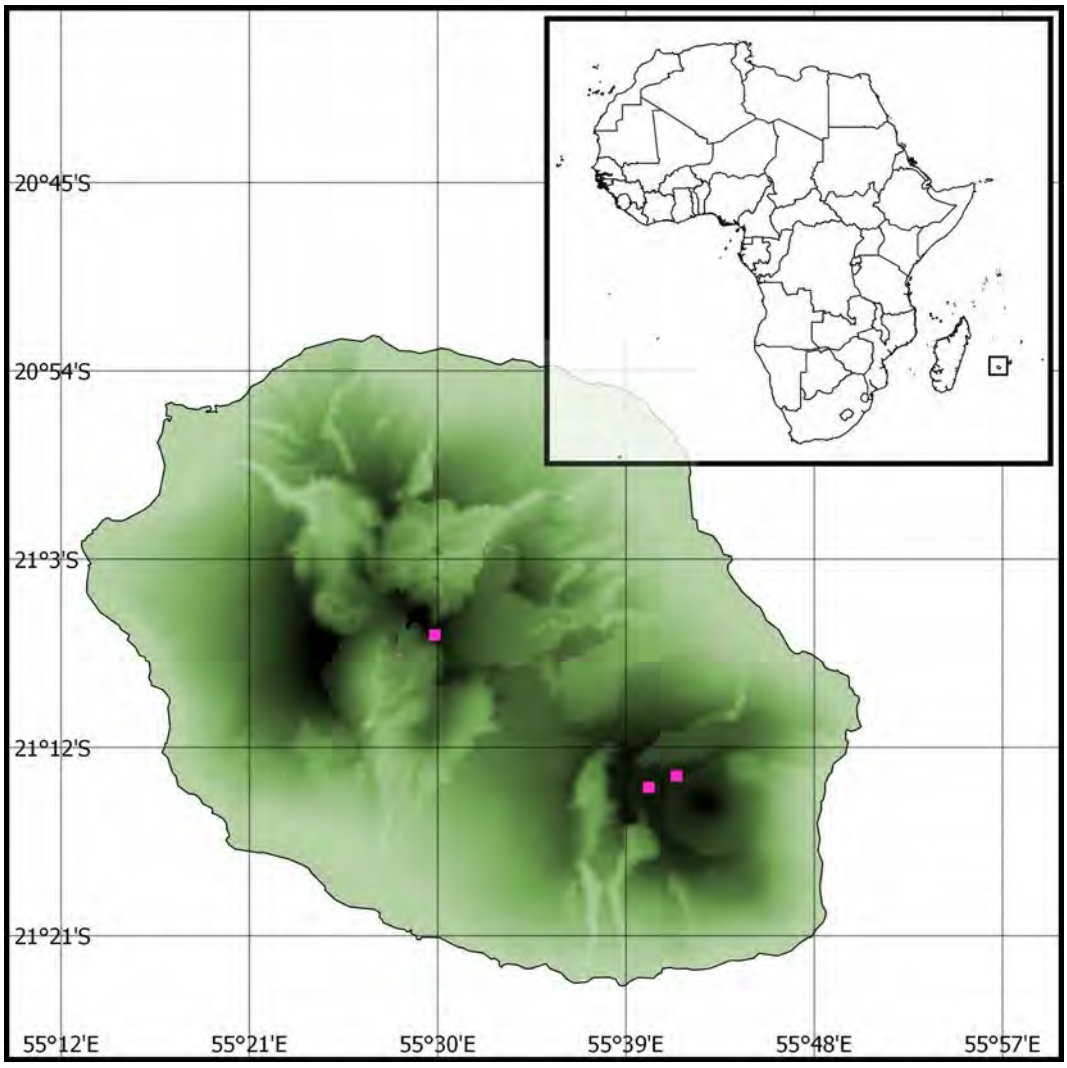

Figure 5.20: Distribution of *E. lepervanchei* in Africa.

Specimens Examined

RÉUNION ISLAND (FRANCE). Piton de la Fournaise, *E. & P. Hegewald 11552*, 1/3/1991 (MO), *N. Wilding 54, 73, 76, 162, 163a, 163b, 163c*, 25/4/2011 (BOL), *J. Bardat REU 1334*, 23/8/2013 (BOL); Cilaos, *R. Marshall & C.A. Crosby 8210*, 29/11/1972 (MO), *F.M. Onraedt Gq.R.315*, 11/12/1969 (EGR), *A. Szabo 9640/CD*, 11/6/1996 (BOL, EGR), *N. Wilding 176*, 3/10/2012 (BOL);

Plaine aux Sables, *C. Ah–Peng & J. Bardat REU1383*, 25/8/2013 (BOL).

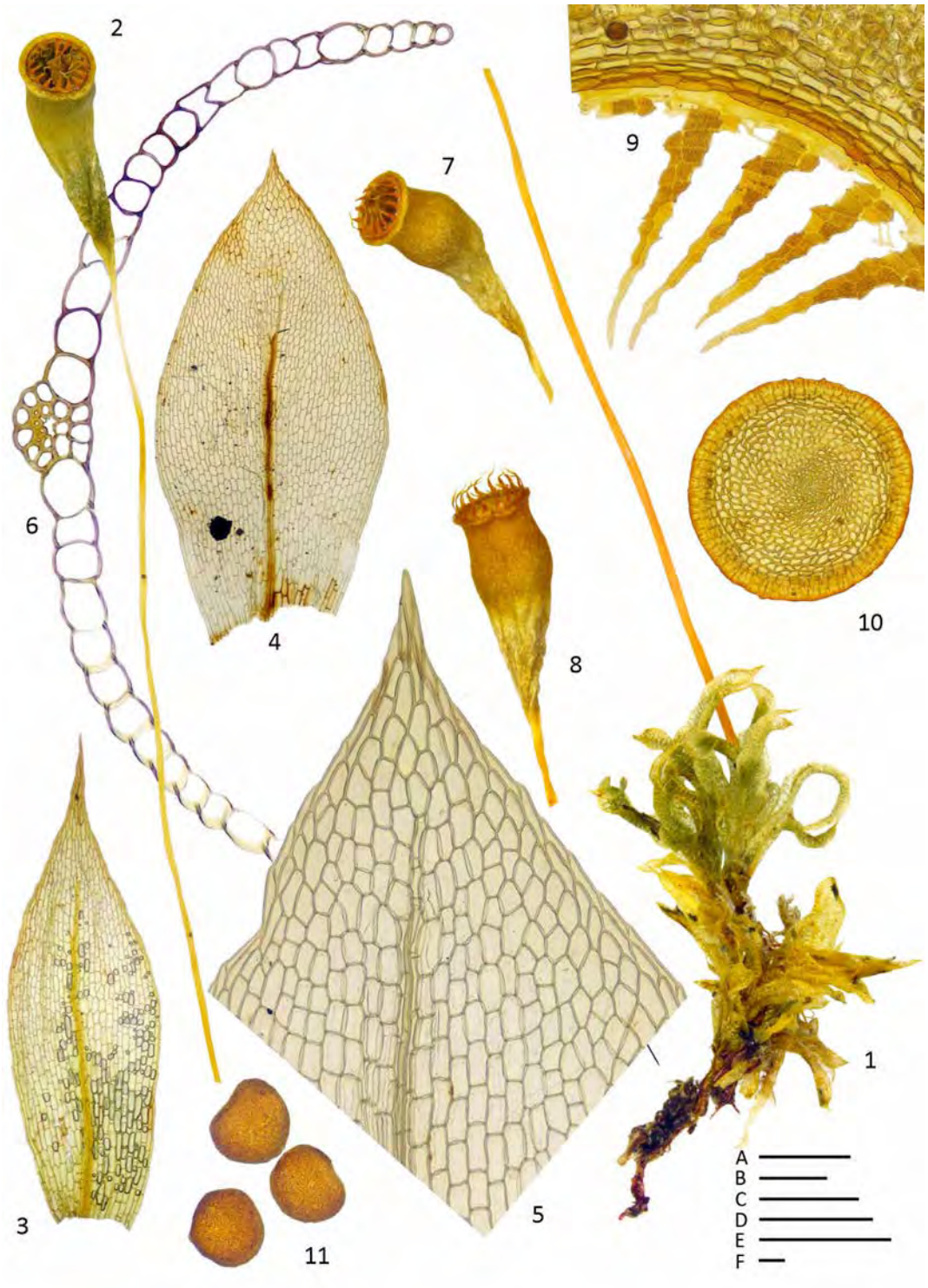

Figure 5.21: *Entosthodon lepervanchei.* 1, 2. Habit, dry (*N. Wilding 176*, BOL); 3, 4. Leaves (3 – *P. Lepervanche s.n.*, PC; 4 – *A. Szabo 9460CD*, BOL); 5. Leaf apex (as for 1 & 2); 6. Leaf cross-section (as for 4); 7, 8. Capsule, dry (as for 1 & 2); 9. Capsule mouth & peristome (as for 1 & 2); 10. Operculum (as for 1 & 2); 11. Spores (*E. & P. Hegewald 11552*, MO). Scale bars: A (3, 4) = 500 µm; B (5, 9) = 100 µm; C (1, 2, 7, 8) = 1 mm; D (6) = 100 µm; E (11) = 50 µm; F (10) = 100 µm.

Entosthodon limbatus Müll. Hal., Bot. Zeitung (Berlin) 16: 155 (1858); *Funaria limbata* (Müll. Hal.) Broth., Nat. Pflanzenfam. [Engler & Prantl] I(3): 524. 1903; 10: 328 (1924).–TYPE : SOUTH AFRICA. Western Cape, Zitskamma [Tsitsikamma], Breutel s.n. (BM, lectotype!, designated here). I suspect that this may be the only existing type specimen and that any others were destroyed during the Allied bombing of Germany in WWII. A specimen in S (B7775) labelled as the co–type is from Clarkson in the Eastern Cape of South Africa, a different locality to the type specimen reported in the protologue which is from Zitskamma [Tsitsikamma]. No mention of additional material from Clarkson is made.

Synonyms:

Entosthodon ampliretis Rehmann ex Müll. Hal., Hedwigia 38:60 (1899). *Funaria ampliretis* (Rehmann ex Müll. Hal.) Broth., Nat. Pflanzenfam. [Engler & Prantl] I(3): 525. 1903; 10: 329 (1924).–TYPE: SOUTH AFRICA. KwaZulu–Natal, Umgeni above Pietermaritzburg, *Rehmann 174* (G, lectotype!, designated here; isolectotypes in PC!, S!, BM!). The original material used by Müller, housed in B along with many of Rehmann's original specimens (in B and Z), was most likely destroyed during the Allied bombing of Germany in WWII. No specimen was located in Z. I have chosen the specimen in G to serve as the lectotype because it conforms to Müller's description and the material is in a good state.

Entosthodon gracilescens Müll. Hal., *hom. illeg*., Hedwigia 38: 59 (1899), non Schwägr. ex Müll. Hal. (1858).–TYPE: SOUTH AFRICA. Transvaal (Mpumalanga), *Wilms s.n.* Feb. 1883 (G, holotype!).

Entosthodon micropyxis Müll. Hal., Hedwigia 38:60 (1899). *Funaria micropyxis* (Müll. Hal.) Broth., Nat. Pflanzenfam. [Engler & Prantl] I(3): 524. 1903; 10:

328 (1924).–TYPE: SOUTH AFRICA. Western Cape, near Blanco, *Rehmann 175* (BM, lectotype!, designated here; isolectotype in G!). The original material used by Müller, housed in B along with many of Rehmann's original specimens (in B and Z), was most likely destroyed during the Allied bombing of Germany in WWII. No specimen was located in Z. I have chosen the specimen in BM to serve as the lectotype because it conforms to Müller's description and the material is in a good state.

Physcomitrium leptolimbatum Müll. Hal., Hedwigia 38:59 (1899).–TYPE: SOUTH AFRICA. Transvaal (Mpumalanga), near Lydenburg, *Wilms s.n.* Feb. 1888 (G, holotype!).

Entosthodon marginatus Müll. Hal., Syn. Musc. 1: 125 (1848).–TYPE: SOUTH AFRICA. Swellendam, *Ecklon s.n.*

Funaria marginata (Müll. Hal.) Broth., hom. Illeg., Nat. Pflanzenfam. [Engler & Prantl] I(3): 525. (1903), non Kindberg (1883).

Entosthodon marginatus var. obtusatus Sim, Bryoph. S. Afr. 297 (1926). *Funaria ampliretis var. obtusata* (Sim) Wijk. & Marg., Taxon 9: 189 (1960).–TYPE: SOUTH AFRICA. KwaZulu–Natal, Umhwati, New Hanover, *Sim 8585* (PRE, holotype!).

Entosthodon mauritianus Schimp ex. Besch., Ann. Sci. Nat., Bot., sér. 6, 9: 375 (1880). *Funaria mauritiana* (Schimp ex. Besch.) Broth., Nat. Pflanzenfam. [Engler & Prantl] I(3): 523 (1903).–TYPE: MAURITIUS. Le Pouce Mt., *Darnty s.n.* Sept 1874 (PC, holotype!).

Funaria holstii Broth., Bot. Jahrb. Syst. 20: 187 (1894). *Entosthodon holstii* (Broth.) Paris, Index Bryol. 424 (1896).–TYPE: TANZANIA. Usambara Mts., *Holst 1054* (H, holotype!).

Funaria usambarica Broth., Bot. Jahrb. Syst. 20: 187 (1894). *Entosthodon usambaricus* (Broth.) Paris, Index Bryol. 427 (1896).–TYPE: TANZANIA. Us-

ambara Mts., Holst 1089 (H, holotype!).

Probable synonyms:

Entosthodon marginatulus Müll. Hal., Abh. Naturwiss. Vereins. Bremen 7: 204 (1882).–TYPE: MADAGASCAR. *Wald von Ambatondrazaka*, 6 Dec. 1877. The type specimen of this name has not been located, it is likely that the only specimen was destroyed during the Allied bombing of Berlin in World War II. Based on its description alone I believe it to be synonymous with *E. limbatus*.

Illustration: Figure 5.23.

Plants small to medium, light–green. *Stems* reddish–brown, to 5 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids cerise. *Leaves* erect–spreading, little contorted to contorted when dry, ovate to spathulate, less frequently ovate–lanceolate, (1.2)1.5–3(3.3) x (0.5)0.75–1.4(1.7) mm, plane to slightly concave, short acuminate to apiculate, entire or more often serrate in upper ½, arista absent; *cells of upper lamina* quadrate to oblong–hexagonal, 40–75 x 17–35 µm; *basal* 62–187(250) x 17–35(45) µm; *marginal cells* narrower, forming a border 1–3 cells wide; *costae* ending below apex, rarely percurrent.

Polyoicous. *Setae* 2.5–12 mm long, straight, pale–yellow to reddish–brown. *Capsules* erect, radially symmetric, pyriform to oblong–obovoid, 1–1.8 x 0.5–0.8 mm, constricted below mouth when dry, yellow to reddish–brown at maturity, with a well differentiated neck *ca*. ½ total length of capsule; *mouth* transverse, *ca*. ⅔ diameter of capsule; *exothecial cells*, 32–68 x 10–18 (25) µm, in cross-section with thick, strongly cuneate anticlinal walls, 3–5 rows of oblate cells

at mouth. *Opercula* plano–convex, cells not twisted or twisted anti–clockwise from above. *Peristome*, single or double, usually single and rudimentary; *exostome teeth*, when well developed, straight to weakly sigmoidal, irregular in shape, orange, to µm 300 high, *ca*. 75 µm wide at base, trabeculate, ornamentation variable, papillose, verrucose–lirate, striate; *endostome teeth*, if present, rudimentary, to 10 µm high and 50–65 µm wide. *Spores* 27.5–37.5 µm, tetrahedral, verrucate–lirate to reticulate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Entosthodon limbatus is characterized by its radially symmetric, peristomate capsules and leaves that are bordered by 1–3 rows of longer, thicker–walled cells.

The leaf margins (mostly lower) can, at times, become folded across the leaf, a feature characteristic of the entire limbate complex in *Entosthodon s.s.*. The only other species treated here falling within this group is *E. borbonicus*.

Habitat and Distribution

Entosthodon limbatus is common across southern and Eastern South Africa, with a single station in Zimbabwe and isolated occurrences in Madagascar and Mauritius (Figure 5.22). It occurs in a wide variety of habitats, in montane fynbos at elevations of *ca*. 500 m in the Western Cape of South Africa to tropical forest at *ca*. 1000 m in Madagascar and Mauritius and at elevations over 2000 m in Zimbabwe.

Note

Entosthodon limbatus is likely a complex of two or more species (See Note under *E. borbonicus*). As currently circumscribed the species occupies a wide distribu-

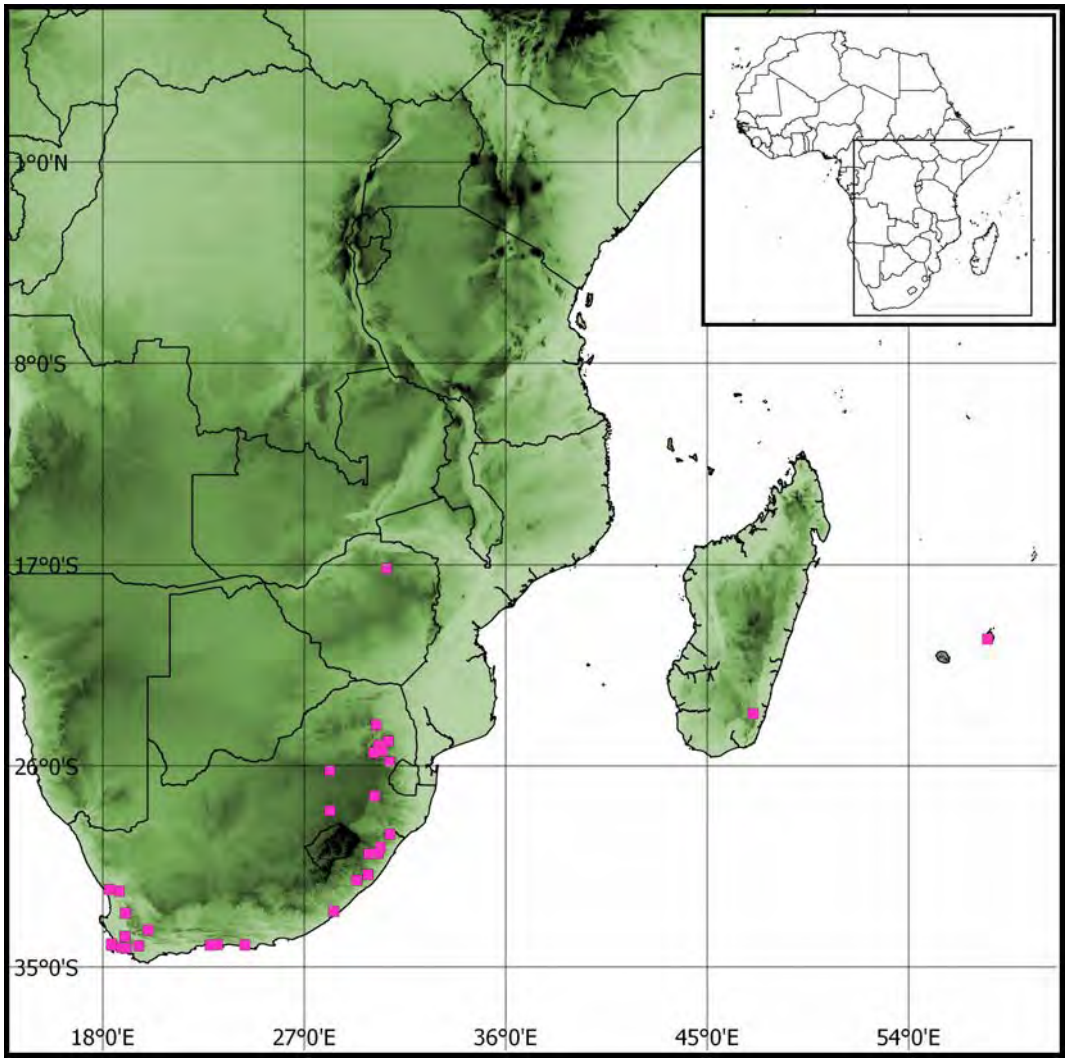

Figure 5.22: Distribution of *E. limbatus* in Africa.

tion, which is not unusual for members of the genus. However, the distribution of *E. limbatus* traverses multiple vegetation types and climatic zones, i.e. Mediterranean, subtropical and tropical. It may not be impossible for a species to achieve such a distribution but the combination of this with a number of morphological inconsistencies point to the presence of a more complex situation possibly involving recent speciation from tropical areas into dryer parts of the continent.

To an extent, the large number of synonyms reflects the variability the species

displays at a morphological level. Margins, for example, are not always clearly differentiated as in the case of *F. holstii*, and degree of peristome development, as is generally the case in *Entosthodon s.l.*, can vary considerably within species. Out of 11 synonyms listed here, 7 are names proposed by Carl Müller. Clearly, by the number of names, Müller too recognized the considerable morphological and ecological variation of the taxon. Phylogenetic evidence (Chapter 2 & 4) suggests a possible recent diversification.

Remnants of a peristome were found on type material of *Funaria holstii*; this and its leaf morphology indicate its relationship to *E. limbatus*.

Specimens Examined

MADAGASCAR. Befotaka Forest, *R. Decary 77*, 16/8/1926 (MO).

MAURITIUS. Curepipe, *D. Lorens 853A*, 13/10/1973 (MO); Le Pouce, *Strasberg & Warren REUD537* (REU).

SOUTH AFRICA. Eastern Cape: Clarkson, *Breutel s.n.* (S:B174687 & B175365); Pondoland, *J. Van Rooy 1836*, 1/2/1985 (PRE, MO); Bizana, *N. Phephu 24*, 23/12/2006 (PRE); Kentani, *A. Pegler 1360*, 1/9/1906 (BOL, PRE); KwaZulu–Natal, Near Kranskop, *B.J. Cholnoky 45, 51, 54*, 22/7/1957 (S); Pietermaritzburg, *J. Van Rooy 1001*, 1/3/1982 (PRE, MO), *A. Rehmann 521* (PRE, BOL), *521b* (BOL); Richmond, *J. Van Rooy 1011*, 1/3/1982 (PRE, MO), *H.A. Wager 287* (PRE); Donnybrook, *E.M. Doidge M4022*(c), 1/8/1933 (PRE); Natal National Park, *H.A. Wager 1478*, (PRE); Goodoo, *H.A. Wager 11703* (PRE); Lekgalameetse N.R., *M. Stalmans 1691*, 1/8/1988 (PRE); Harding, *T.A.J. Hedderson 15505*, 8/1/2004 (BOL); Limpopo: Zoutpansberg, *P. Thomas 2961*, 30/4/1931 (MO); Mpumalanga: Barberton, *K.H. Rechinger 5220*, 16/10/1963; Wakkerstroom, *H. Toelken 5737*, 21/2/1978 (MO); Lydenburg, *J.M. Rankin 54*, 9/9/1976 (MO); Pilgrimsrest, *A. Rehmann 521b*, (PRE); Western Cape, Blaauwberg, *E. Es-*

terhuysen 21561, 1/6/1953 (S; BOL); Cape Town, *S. Arnell 317*, 6/9/1951 (S), *932*, 22/3/1951 (S:B174679); Grabouw, *B.J. Cholnoky 417A*, 2/10/1956 (S; MO) Genadendal *A. Rehmann 521* (S); Koekenaap, *K.H. Rechinger 5108*, 16/9/1963 (S); Wellington, *S.M. Perold 1177*, 11/9/1986 (PRE, MO), Sedgefield, *T.A.J. Hedderson 16985*, 5/5/2009 (BOL), *N. Wilding 172*, 7/10/2010 (BOL); Citrusdal, *T.A.J. Hedderson 13684*, 17/2/2001 (BOL); Cederberg, *T.A.J. Hedderson 13094, 13105*, 27/2/2000 (BOL); Touws River, *N. Wilding HBCT305a, HBCT305b*, 5/9/2011 (BOL).

ZIMBABWE. Inyanga, *J.E. Rushworth 915*, 29/4/1967 (MO); Makonde, E.B. Best OT39, 19/7/1987 (MO).

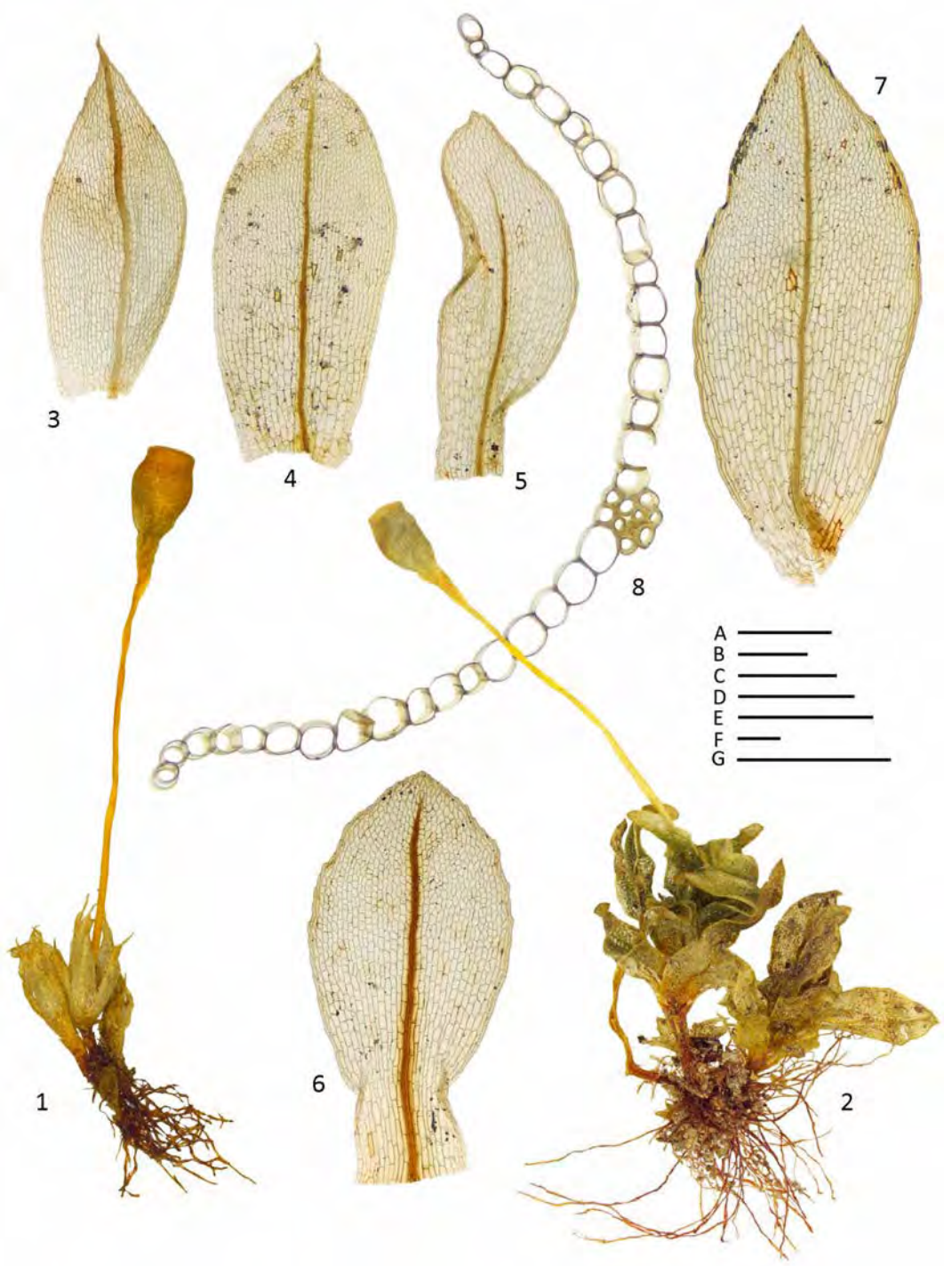

Figure 5.23: *Entosthodon limbatus*. 1, 2. Habit, dry (1 – *M. Stalmans 1691*, PRE; 2 – *N. Wilding 215*, BOL); 3–7. Leaves (3 – *N. Wilding 160*, BOL; 4 – *N. Wilding 216*, BOL; 5, 7 – *P. Thomas 2961*, MO; 6 – *T.R. Sim 8585*, PRE); 8. Leaf cross-section (*T.A.J. Hedderson 17489*, BOL); 9–12. Capsule, dry (9, 10 – as for 1; 11 – *Strasberg & Warren REUD537*, REU; 12 – as for 2); 13, 14. Capsule mouth & peristome (13 – as for 3; 14 – as for 2); 15. Operculum (as for 3); 16. Spores (*J.E. Rushworth 915*, MO). Scale bars: A (3–7) = 500 µm; B (13, 14) = 100 µm; C (1, 2) = 1 mm; D (8) = 100 µm; E (16) = 50 µm; F (15) = 100 µm; G (9–12) = 1 mm.

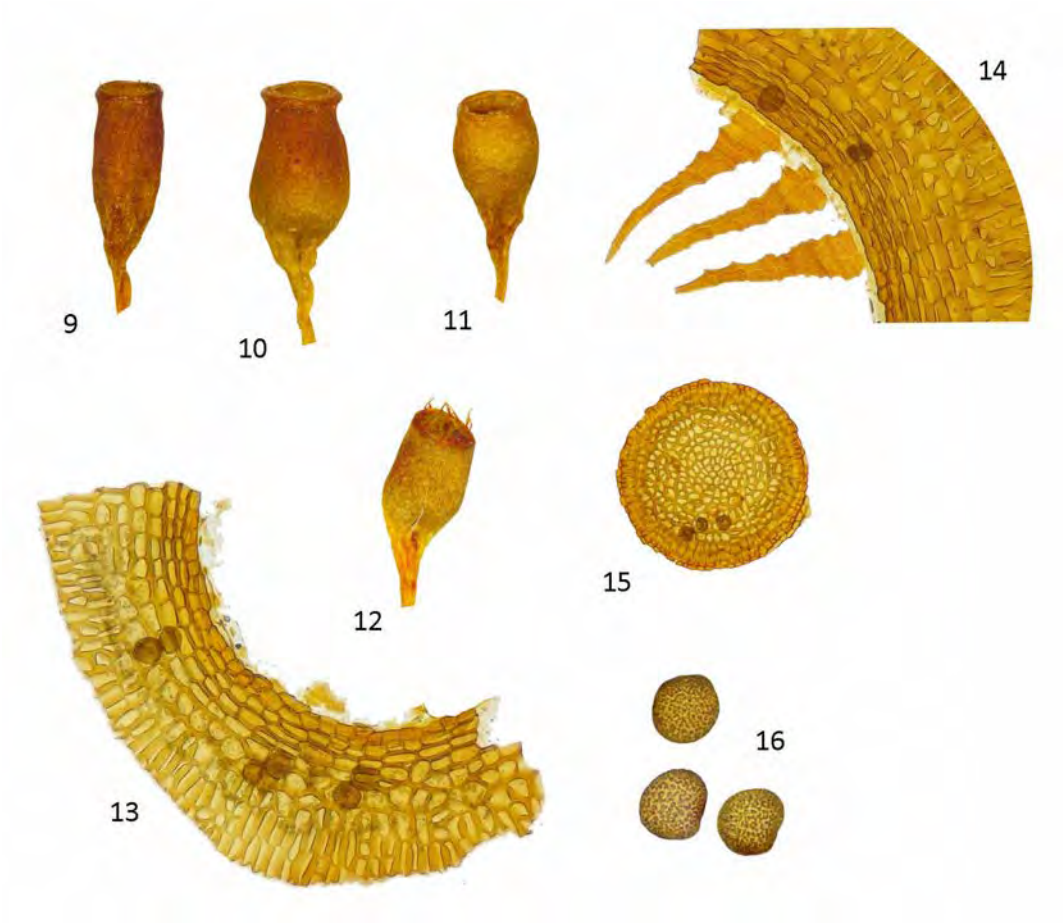

Figure 5.23: (continued).

Entosthodon pertenellus (Broth.) Kis, Proc. Third Meeting Bryol. C. & E. Europe 220 (1984). *Funaria pertenella* Broth.,Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-naturwiss. Kl. 88: 737. 1913.–TYPE: TANZANIA. West Usambara, Kalange, 1000–1100 m. *J. Brunnthaler s.n*. (H, lectotype!; isolectotype in WU!). I have chosen the collection from H to serve as the lectotype as it is home to Brotherus's herbarium. I believe Brotherus could have returned some of the original collection to WU because his specimen at H is too small and in too poor a condition to have been used to generate his detailed account of the species.

Illustration: Figure 5.25.

Plants small, light–green. *Stems* reddish-brown, to 4 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled reddish-brown cortical cells, a hyalodermis and a central strand, rhizoids cerise. *Leaves* erect–spreading, little contorted when dry, ovate to oblong–obovate, 1.1–1.8 x 0.4–0.9 mm (including arista), slightly concave, short acuminate, rarely appearing apiculate, apex entire to weakly serrate above, aristate or not, arista if present to 500 µm; *cells of upper lamina* quadrate to oblong–hexagonal, (22)30–55 (63) x 12–25(30) µm; *basal* (43)75–100(125) x 20–38 µm; *marginal cells* usually undifferentiated, sometimes forming a ± conspicuous border between shoulders and apex; *costae* often excurrent.

Polyoicous. *Setae* 5–7 (15) mm long, straight, reddish–brown. *Capsules* erect or weakly inclined, radially symmetric or with slight bend in neck, pyriform to oblong–pyriform, 1.1–1.9 x 0.4–0.6 mm, weakly constricted below mouth when dry, yellow to reddish–brown at maturity, with a well differentiated neck *ca*. ⅓–½ total length of capsule; *mouth* transverse, *ca*. ¾ diameter of capsule; *exothe-*

cial cells, 40–65 x 8–18 µm, in cross-section with thick, strongly cuneate anticlinal walls, 4–6 rows of oblate cells at mouth. *Opercula* plano–convex, cells not twisted. *Peristome* usually absent, if present consisting of a highly reduced and fragmented hyaline membrane. *Spores* 25–33 µm, tetrahedral, finely verrucate or smooth, trilete scars rarely obvious. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Entosthodon pertenellus can be distinguished from other African species by its eperistomate capsules, nearly smooth spores and leaves that are erect and scarcely contorted when dry, with an excurrent costa.

Habitat and Distribution

The species is known from the high mountains of Grand Comore, Malawi, Réunion Island and Tanzania (Figure 5.24). *Entosthodon pertenellus* occurs at elevations between 1400 m and 3000 m in fairly flat areas in ericaceous vegetation, often alongside water courses or footpaths and in areas which are temporarily flooded.

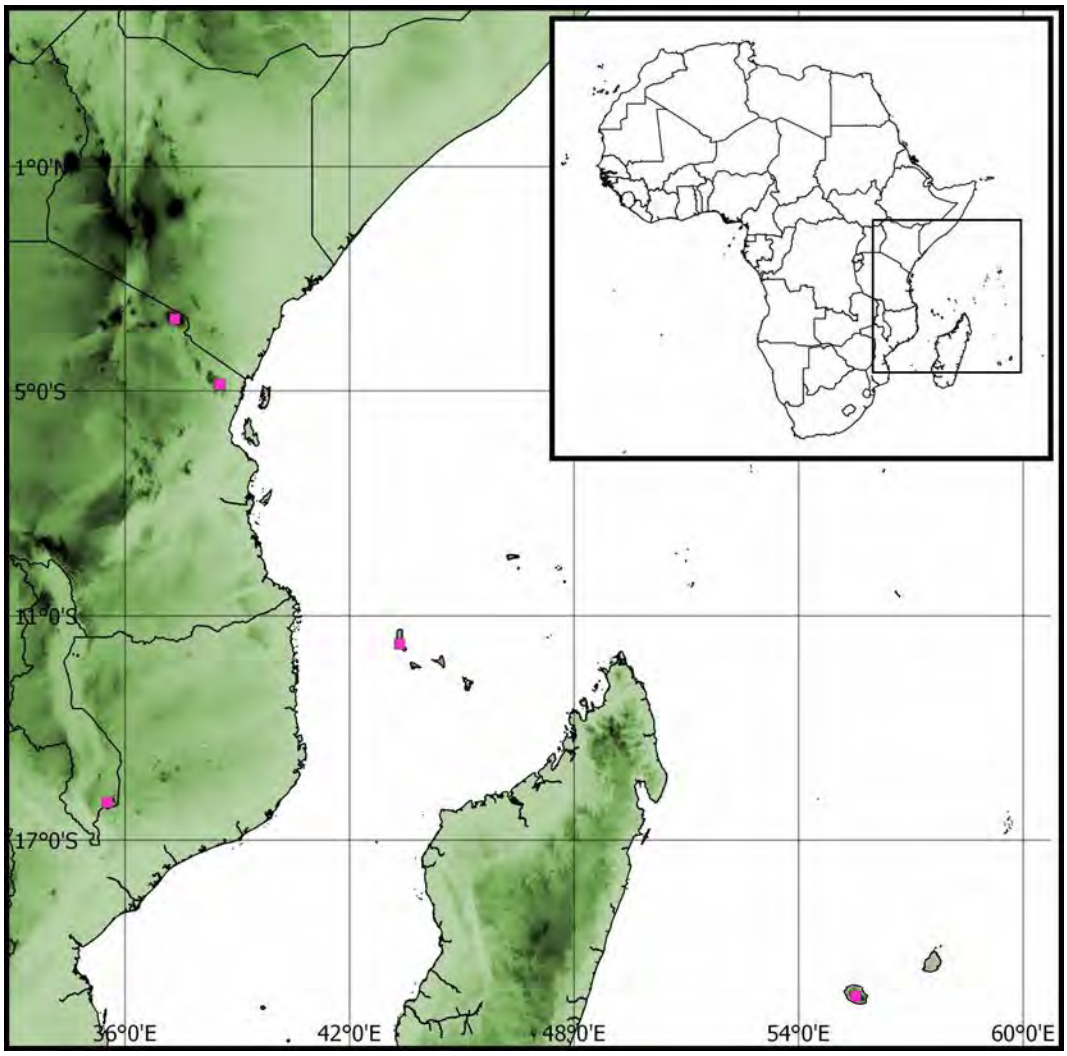

Figure 5.24: Distribution of *E. pertenellus* in Africa.

Note

Over its distribution, *E. pertenellus* exhibits variation largely in the degree to which the marginal cells are differentiated between the apex and shoulder of the leaf. The Malawian material is probably the most extreme in this respect and the leaves often have a distinct, sometimes toothed, border between the apex and shoulders of the leaf (Wilding et al., 2013). Tanzanian and Island (Réunion and Grande Comore) plants are the most similar morphologically while the Malawian

plants are, in general, slightly larger and in addition offer a more or less cohesive set of characters which could justify recognition at a sub-specific level. Phylogenetic analyses (Chapter 2, Wilding et al,. unpublished) are, however, unable to resolve the relationship among these major populations suggesting either recent dispersal or some degree of gene flow between populations.

Specimens Examined

COMOROS. Grande Comore (Ngazidja), Karthala, *T. Pócs 9159/AL*, 19/3/1991 (BOL, EGR, SUA).

MALAWI. Mulanje, *T.A.J. Hedderson 17420, 17440a, 17441*, 9/6/2010, *17491,* 11/6/2010, *17495*, 12/6/2010, *17478,* 10/6/2010 (BOL).

RÉUNION ISLAND (FRANCE). Piton des Neiges, *T.A.J. Hedderson 16634b,* 24/3/2008, *16636, 16637*, 26/3/2008 (BOL), *N. Wilding 182, 185*, 3/10/2011, *237*, 3/5/2011, *77, 166, 167*, 4/5/2011 (BOL), *Ah-Peng et al 2000P1Q2Te2*, 26/5/2008 (REU); Roche Ecrit, *T.A.J. Hedderson 16580,* 11/12/2007 (BOL), *N. Wilding 55, 59, 56, 61*, 26/4/2010 (BOL); Maido, N. Wilding 20, 22b, 22c, 23, 32, 33, 35, 40, 13/4/2010 (BOL), *Ah–Peng & Hedderson R584.9*; Mafate, *N. Wilding 151,* 2/5/2010 (BOL); Route du Volcan, *N. Wilding 30a, 31, 71*, 3/4/2010; Cratère Commerson, *N. Wilding 75, 155, 156, 164, 165*, 25/4/2011; Pas de Bellecombe, *N. Wilding 64, 67*, 25/4/2010, *J. Bardat REU 1352*, 9/9/2013 (BOL).

TANZANIA. Kilimanjaro Mt. *T. Pócs, R. Ochyra & H. Bednarek–Ochyra, 88124/M, 88125/ST, 88118/V, 88125W,* 15/6/1988 (BOL, EGR, SUA).

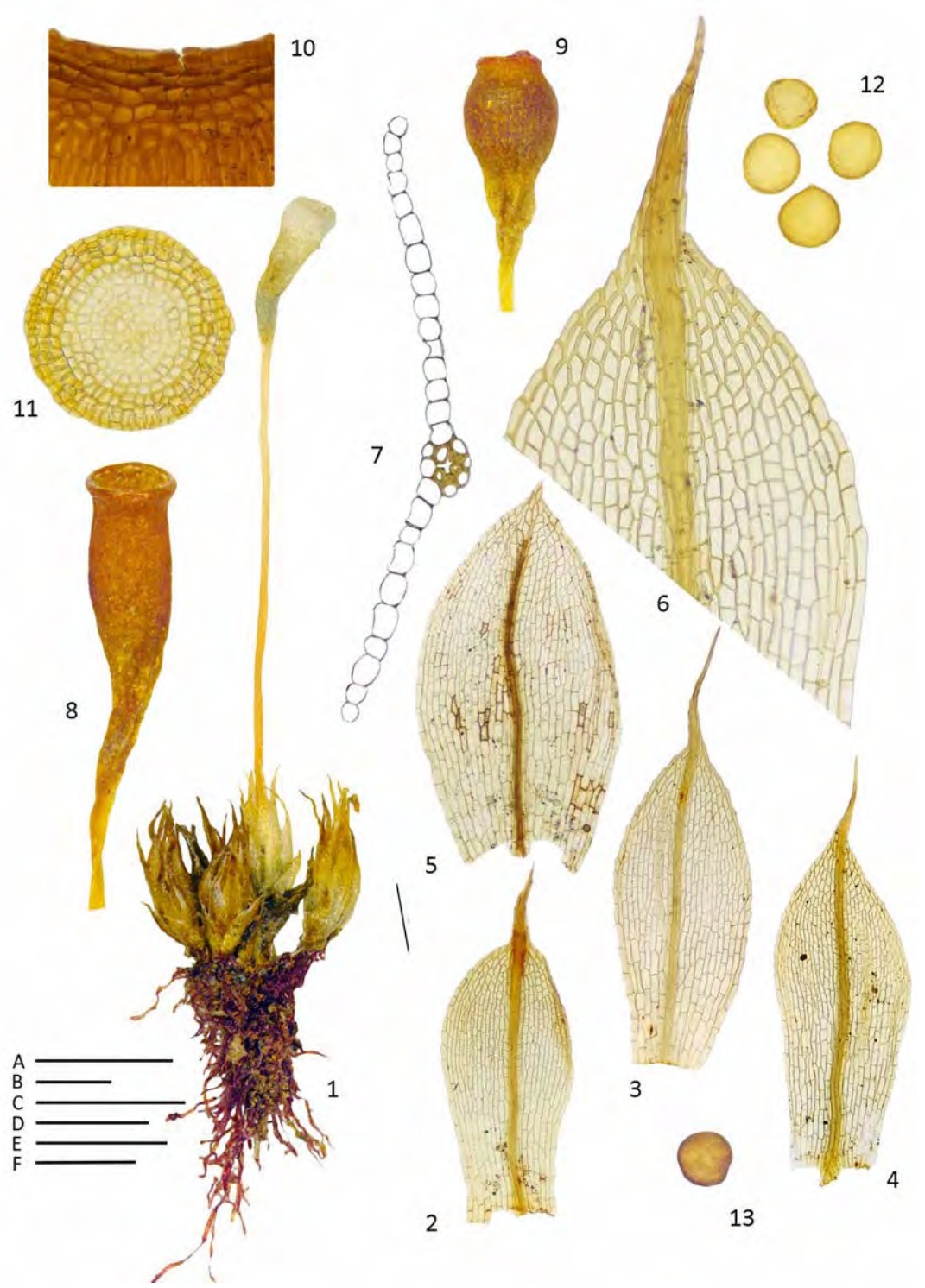

Figure 5.25: *Entosthodon pertenellus.* 1. Habit, dry (*N. Wilding 64*, BOL); 2–5. Leaves (2 – *N. Wilding 165*, BOL; 3 – *T.A.J. Hedderson 17420* , BOL; 4 – *N. Wilding 156*, BOL; 5 – *Ah–Peng et al. 2000P1Q2Te2*, REU); 6. Leaf apex (*N. Wilding 75*, BOL); 7. Leaf cross-section (*N. Wilding 164*, BOL); 8, 9. Capsule, dry (8 – *T.A.J. Hedderson 17491*, BOL; 9 – *N. Wilding 61*, BOL); 10. Capsule mouth (as for 5); 11. Operculum (*N. Wilding 151*, BOL); 12, 13. Spores (12 – *N. Wilding 40*, BOL; 13 – as for 5). Scale bars: A (2–5) = 500 µm; B (6, 10, 11) = 100 µm; C (1) = 1 mm; D (7) = 100 µm; E (12, 13) = 50 µm; F (8, 9) = 500 µm.

Entosthodon pocsii N. Wilding sp. nov.–TYPE: TANZANIA. Njombe Distr., Kipengere range, between Mt Ishinga and Sanshashi Hill, 2400–2600 m, *S. Iversen, E. Persson, B. Petterson & T. Pócs, 87145/D*, 26 May 1987 (BOL, holotype!; isotype in EGR).

The species is named in honour of Tamas Pócs for his work on the African bryophyte flora.

Illustration: Figure 5.27.

Plants small, light–green. *Stems* reddish-brown, to 5 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids cerise. *Leaves* erect–spreading, little contorted when dry, ovate to oblong–obovate, 1.2–2 x 0.4–0.9 mm, concave, short acuminate, entire, aristate or not, arista if present to 400 µm; *cells of upper lamina* quadrate to oblong–hexagonal, 23–55 x (10)15–30(35) µm; *basal* 62–150(188) x (15)20–35(43) µm; *marginal cells* longer and narrower near apex; *costae* ending below apex to excurrent.

Polyoicous. *Setae* 5–7 mm long, straight, pale–yellow to reddish–brown. *Capsules* erect to inclined, radially symmetric or with slight bend in neck, oblong-pyriform, 1.2–1.7 x 0.5–0.8 mm, weakly constricted below mouth when dry, yellow to reddish–brown at maturity, with a well differentiated neck *ca*. ½ total length of capsule; *mouth* transverse, *ca*. ⅔ diameter of capsule; *exothecial cells* (30)4–68 x 10–20 µm, in cross-section with thick, strongly cuneate anticlinal walls, 3–6 rows of oblate cells at mouth. *Opercula* plano–convex, cells not or slightly twisted anti–clockwise from above; *peristome* double and rudimentary; *exostome teeth* straight, irregular in shape, orange, tapered to an acute or rounded apex, sometimes becoming hyaline in upper ⅓, to 175 µm high and 60 µm wide

at base, finely papillose to verrucate–lirate, trabeculate, weakly appendiculate; *endostome teeth* rudimentary, smooth, hyaline, to 40 µm high and 22 µm wide. *Spores* 27–38 µm, tetrahedral, finely papillose–lirate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Entosthodon pocsii can be distinguished by its ± upright, radially symmetric, peristomate capsules and finely verrucate–lirate spores. Macroscopically, the species may be confused with *E. bergianus*. However, their spore ornamentations differ and *E. bergianus* is generally larger and the leaf costa is never excurrent.

Habitat and Distribution

The species is known from only three collections in Tanzania (Figure 5.26), two in the Kipengere Range and one from Arusha National Park, where it occurs at high elevations *ca*. 2700 m.

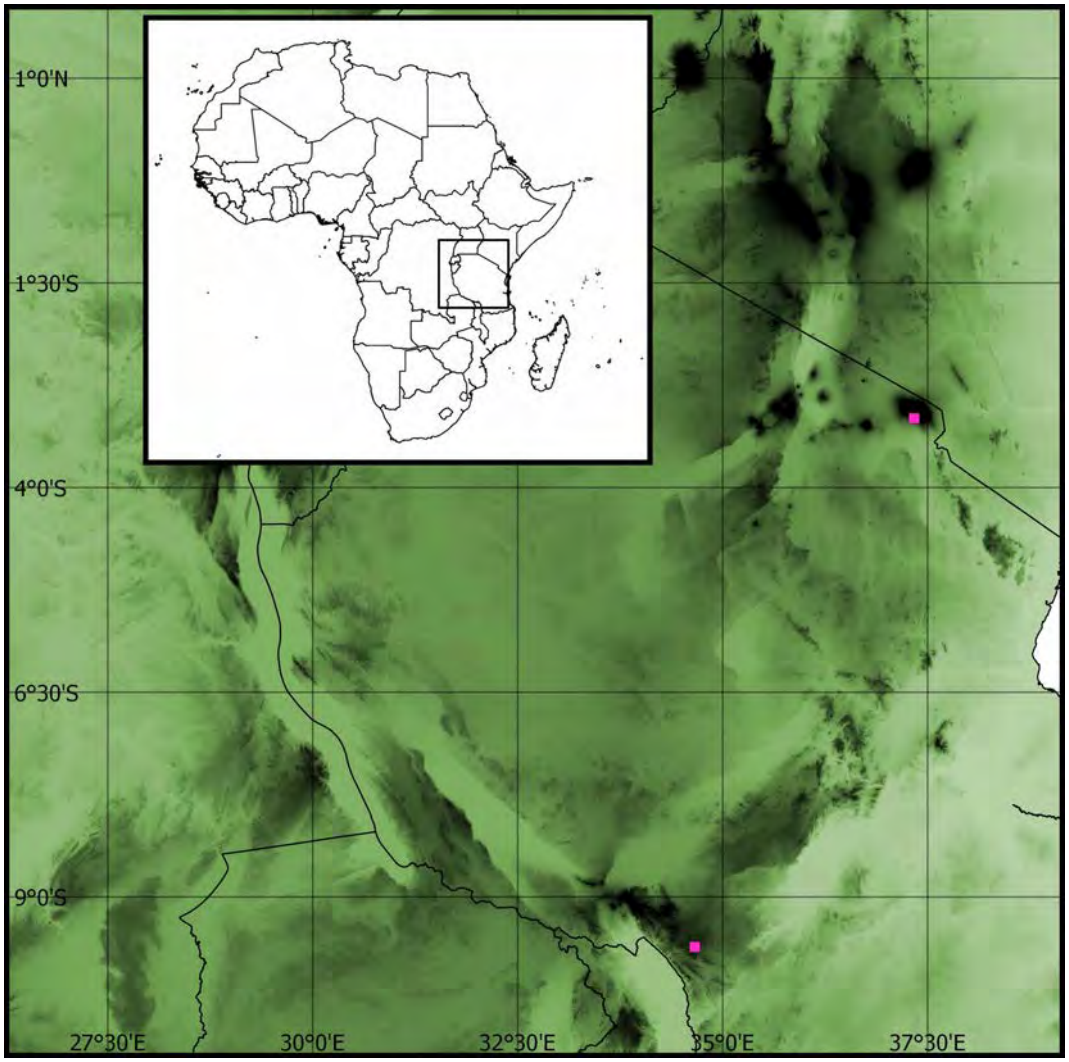

Figure 5.26: Distribution of *E. pocsii* in Africa.

Note

Phylogenetic analyses (see Chapter 2) place *E. pocsii* sister to another African endemic *E. pertenellus*. The two species share a similar habitat and both species posses a leaf architecture that can be highly variable among populations.

Specimens Examined

TANZANIA. Arusha N.P., *T. Pócs, D. Harrison & J.M. Mushy 90130/UV*, 9/6/1990

(BOL, EGR); Njombe Distr., Kipengere Range, *S. Iversen, E. Persson, B. Petterson & T. Pócs 87145/N*, 26/5/1987 (BOL, EGR); Arusha N.P., *T. Pócs, D. Harrison & J.M. Mushy 90130/UV*, 9/6/1990 (BOL, EGR, SUA).

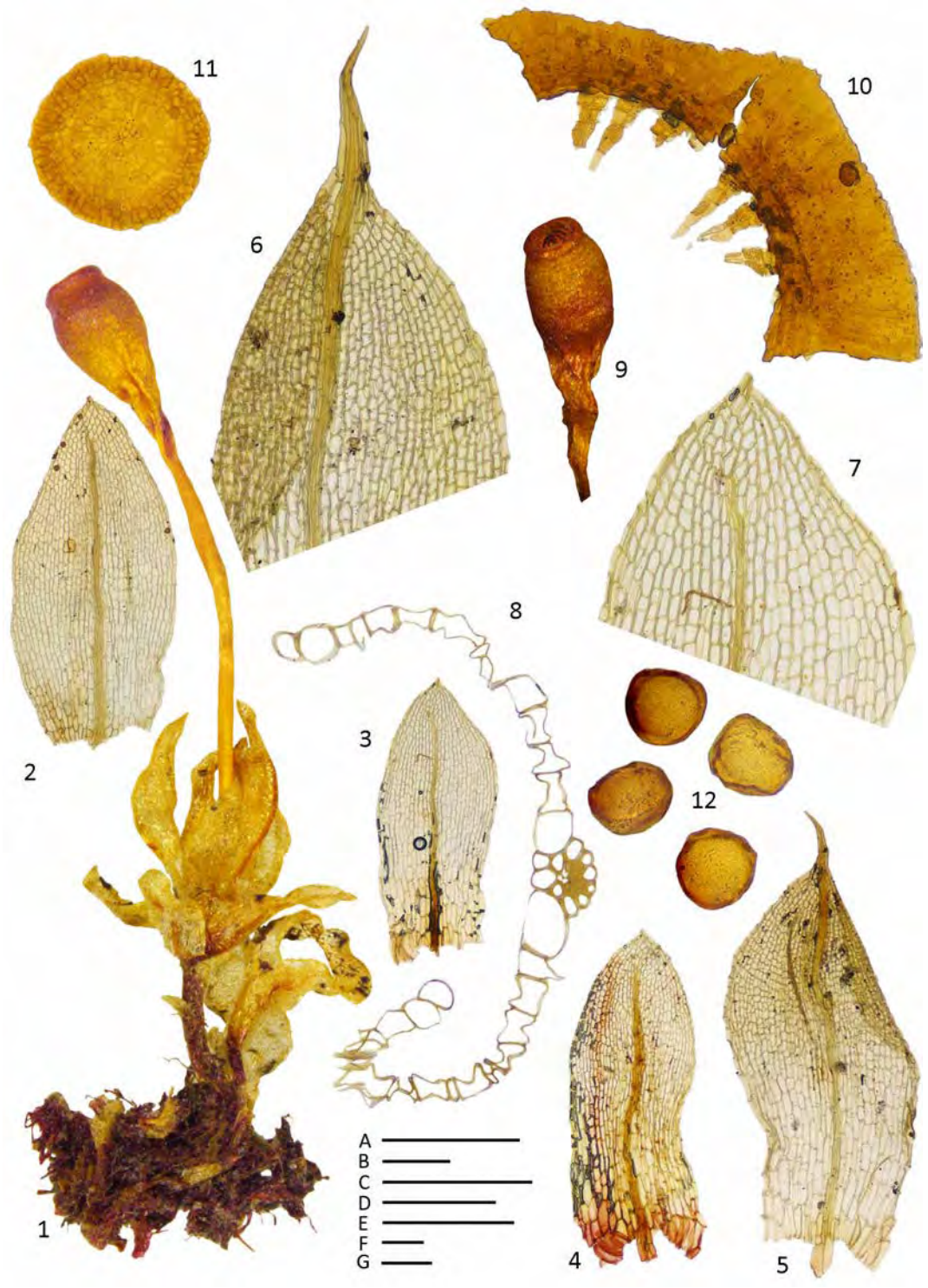

Figure 5.27: *Entosthodon pocsii.* 1. Habit, dry (*S. Iversen, E. Persson, B. Petterson & T. Pócs, 87145/D*, BOL); 2–5. Leaves (2 – as for 1 ; 3–5 – *S. Iversen, E. Persson, B. Petterson & T. Pócs, 87145/N*, BOL); 6, 7. Leaf apex (6 – as for 1 ; 7 – as for 3); 8. Leaf cross-section (as for 3); 9. Capsule, dry (*T. Pócs, D. Harrison & J.M. Mushy 90130/UV*, (BOL, EGR); 10. Capsule mouth & peristome (as for 3); 11. Operculum (as for 1); 12. Spores (as for 1). Scale bars: A (2–5) = 500 µm; B (10) = 100 µm; C (1, 9) = 1 mm; D (8) = 100 µm; E (12) = 50 µm; F (11) = 100 µm; G (6, 7) = 100 µm.

Entosthodon rhomboideus (J. Shaw) N. Wilding, *Funaria rhomboidea* J. Shaw, Cape Monthly Mag. 17: 315 (1878). –TYPE: SOUTH AFRICA. Eastern Cape, near Graaff-Reinet, *McLea s.n.*, *sub Rehmann 523*. (BOL, lectotype!, designated here; isolectotype in BOL! (*Rehmann 523b*), NH). Multiple duplicates of Rehmann's original collection exist. Hence, I here designate the BOL specimen to serve at the lectotype for the species.

Synonyms:

Entosthodon schinzii Geh., Bull. Herb. Boissier 4: 411 (1896). Funaria schinzii (Geh.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1: 519 (1903).–TYPE: SOUTH–WEST AFRICA (NAMIBIA). Comagas, *Schinz s.n.*, 24 Apr.1885 (Z, lectotype!, designated here). Geheeb's original specimens were likely destroyed during the Allied bombing of Germany during WWII. I have therefore chosen the only other type specimen known, from Z, to serve as the lectotype for *E. schinzii*.

Entosthodon rivale Geh., Bull. Herb. Boissier 4: 411 (1896). *Physcomitrium rivale* (Geh.) Broth., Nat. Pflanzenfam. [Engler & Prantl] 1: 519 (1903).–TYPE: SOUTH-WEST AFRICA [NAMIBIA]. *Schinz s.n.*, Apr.1885 (Z, lectotype!, designated here; isotype in S!). Geheeb's original specimens were likely destroyed during the Allied bombing of Germany during WWII. I have therefore chosen the type specimen from Z to serve as the lectotype as it conforms to Geheeb's description of *E. rivale* and the material is in good condition.

Illustration: Figure 5.29.

Plants medium, pale to dark–green. *Stems* reddish-brown, to 3 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 lay-

ers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids orange or reddish-brown. *Leaves* erect–spreading, contorted when dry, ovate to oblong–obovate or spathulate (1.6)2–3(3.75) x 0.75–1.25(1.9) mm, slightly concave, short–acuminate to apiculate, often bluntly–toothed by projecting cells in upper ½, rarely entire, arista absent; *cells of upper lamina* rhomboidal to oblong–hexagonal, 38–90 x 28–45 µm; *basal* (63) 83–188 (255) x 25–50 µm; *marginal cells* undifferentiated; *costae* ending below the apex.

Polyoicous. Setae 4–6 mm long, straight, orange–brown. *Capsules* erect to inclined, radially symmetric, oblong–pyriform, 1–1.5 x 0.5–0.75 mm, weakly constricted below mouth when dry, yellow to brown at maturity, with a well differentiated neck *ca*. ⅓–½ total length of capsule; *mouth* transverse *ca*. ¾ diameter of capsule; *exothecial cells* 35–63(70) x 10–18 µm, in cross-section with thick, strongly cuneate anticlinal walls, 4–5 rows of oblate cells at mouth. *Opercula* short conic, cells twisted anti–clockwise from above. *Peristome* double; *exostome teeth* straight, irregular in shape, orange, tapered to an acute or rounded apex, to 150 µm high, *ca*. 70 µm wide at base, papillose, striate, trabeculate; *endostome teeth* rudimentary, smooth, segments irregular in shape and hyaline, to *ca*. 63 µm high and 85 µm wide. *Spores* 25–35(40) µm, tetrahedral, weakly papillose or papillose–lirate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

The dentate leaves with costa ending below the leaf apex and strongly papillose to papillose–lirate spores distinguish *E. rhomboideus* from other African species.

Habitat and Distribution

Entosthodon rhomboideus is known from the Northern, Western and Eastern Cape Provinces of South Africa and from southern–central Namibia (Figure 5.28).

The species has been collected in a number of different vegetation types including the Khomas highland savannah of Namibia and Nama–Karoo vegetation in South Africa. *Entosthodon rhomboideus* occurs at elevations between 200 m and 1500 m.

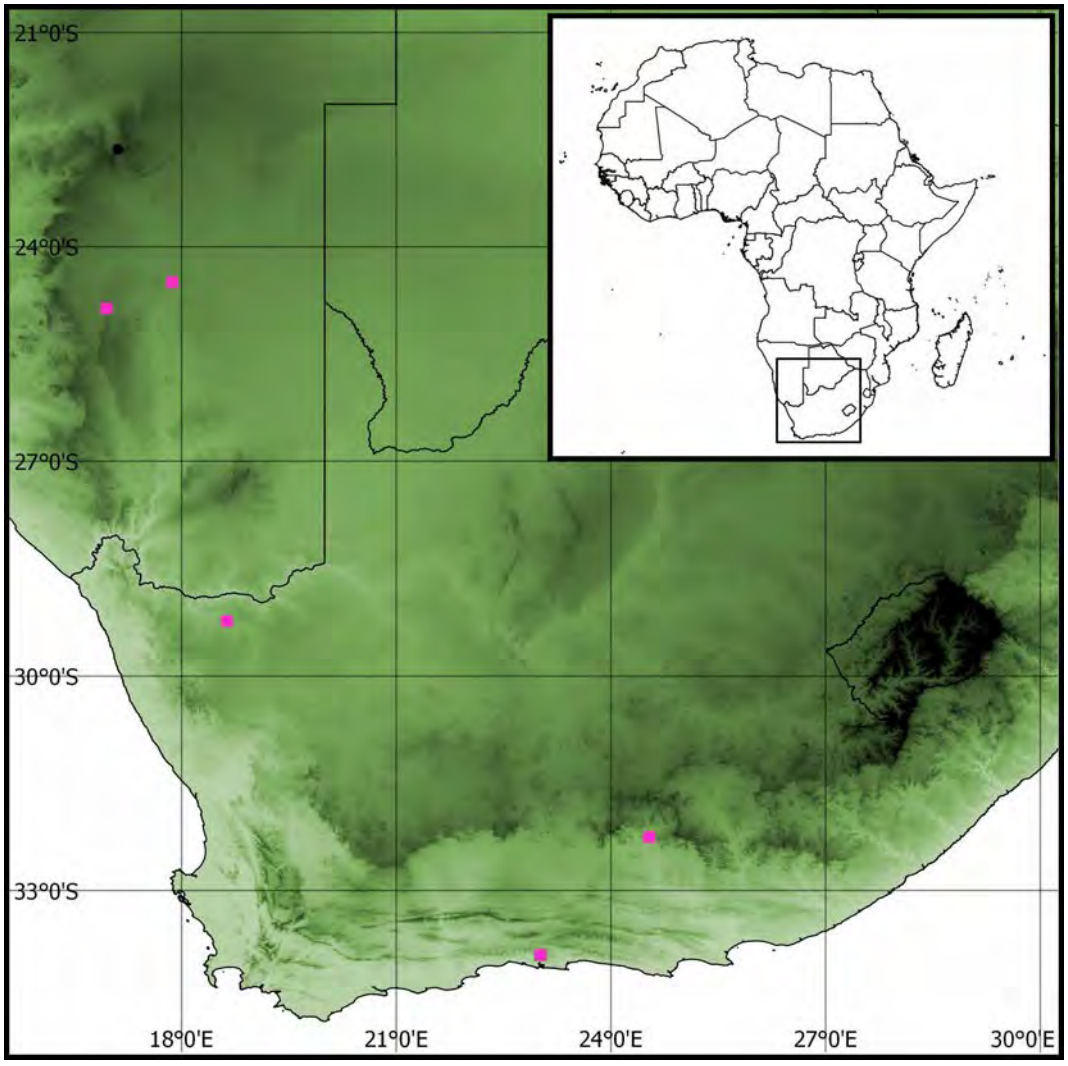

Figure 5.28: Distribution of *E. rhomboideus* in Africa.

Note

The Namibian populations have bigger, often more spathulate, leaves in comparison to the South African populations, and the plants are often a pale green when dry.

Specimens Examined

NAMIBIA. Windhoek, *O.H. Volk 481* (PRE, MO); Maltahöhe, *O.H. Volk 1286*

(PRE); Hardap dam, *C.A. Mannheimer 246*, 28/3/1996 (PRE);
SOUTH AFRICA. Eastern Cape: Graaf Reinet, *N. Wilding 240, 241*, 28/4/2013 (BOL), *Maclea 3062, 3062a* (PRE); Northern Cape: Bushman's Land, *T.A.J. Hedderson 13203*, 21/4/2000 (BOL); Western Cape: Knysna, *Lubenau SA13913*, 12/9/1990 (MO).

Figure 5.29: *Entosthodon rhomboideus.* 1. Habit, dry (*T.A.J. Hedderson 13203,* BOL); 2–4. Leaves (2, 3 – as for 1; 4 – *O.H. Volk 481*, PRE); 5, 6. Leaf apex (5 – as for 1; 6 – *O.H. Volk 1286*, PRE); 7. Capsule, dry (as for 6); 8. Capsule mouth & peristome (as for 4); 9. Operculum (as for 4); 10. Spores (as for 6). Scale bars: A (2–4) = 500 µm; B (5, 6, 8) = 100 µm; C (1, 7) = 1 mm; D (10) = 50 µm; E (9) = 100 µm.

Entosthodon zygolimbatus N. Wilding sp. nov.–TYPE: SOUTH AFRICA. Mpumalanga, Dullstroom, 14 km north on Verlorenvallei farm, elev. 2010 m, *B.K. Drews 19*, 14/10/1980 (PRE, holotype!; isotype in MO!).

The combination of zygomorphic capsules and limbate leaf margins gives this species its name.

Illustration: Figure 5.31.

Plants medium, light–green. *Stems* reddish–brown, to 5 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids cerise. *Leaves* erect–spreading, contorted when dry, oblong obovate to spathulate, 2.2–3 x 1.1–1.5 mm, plane to slightly concave, short acuminate to apiculate, entire to weakly serrate in upper ⅓, arista absent; *cells of upper lamina* rectangular or rhomboidal to oblong–hexagonal, 45–63 x 25–38 µm; *basal* 112–225 x 25–38 µm; *marginal cells* narrower, thicker–walled, forming a border 1–2 cells wide, infrequently undifferentiated; *costae* ending below apex.

Polyoicous. *Setae* 8–16 mm long, straight to slightly curved, reddish–brown. *Capsules* erect to inclined, weakly gibbous, zygomorphic, oblong-pyriform, 1.5–2.1 x 0.5–0.8 mm, weakly constricted below mouth when dry, yellow to reddish–brown at maturity, with a well differentiated neck *ca*. ½ total length of capsule; *mouth* slightly oblique, *ca*. ¾ diameter of capsule; *exothecial cells* 32–53 x 15–23 µm, in cross-section with thick, strongly cuneate anticlinal walls, 4–5 rows of oblate cells at mouth. *Opercula* not seen. *Peristome* single (possibly double, see below); *exostome teeth* straight, regular in shape, orange, to 230 µm high, *ca*. 60 µm wide at base, striate, trabeculate. *Spores* 25–28 µm, tetrahedral, verrucate. *Calyptrae* not seen.

Diagnostic Features

The strongly limbate, dentate leaves and zygomorphic, gibbous capsules clearly distinguish *E. zygolimbatus* from other African species.
The peristome morphology of this species, in particular exostome shape and ornamentation, and whether or not an endostome is present, remains slightly obscure because of a lack of well preserved capsules in the only two known collections.

Habitat and Distribution

The species is known from only two localities, one in South Africa and one in Tanzania (Figure 5.30). *Entosthodon zygolimbatus* is recorded from altitudes between 2000 m and 2400 m in tropical and subtropical zones.

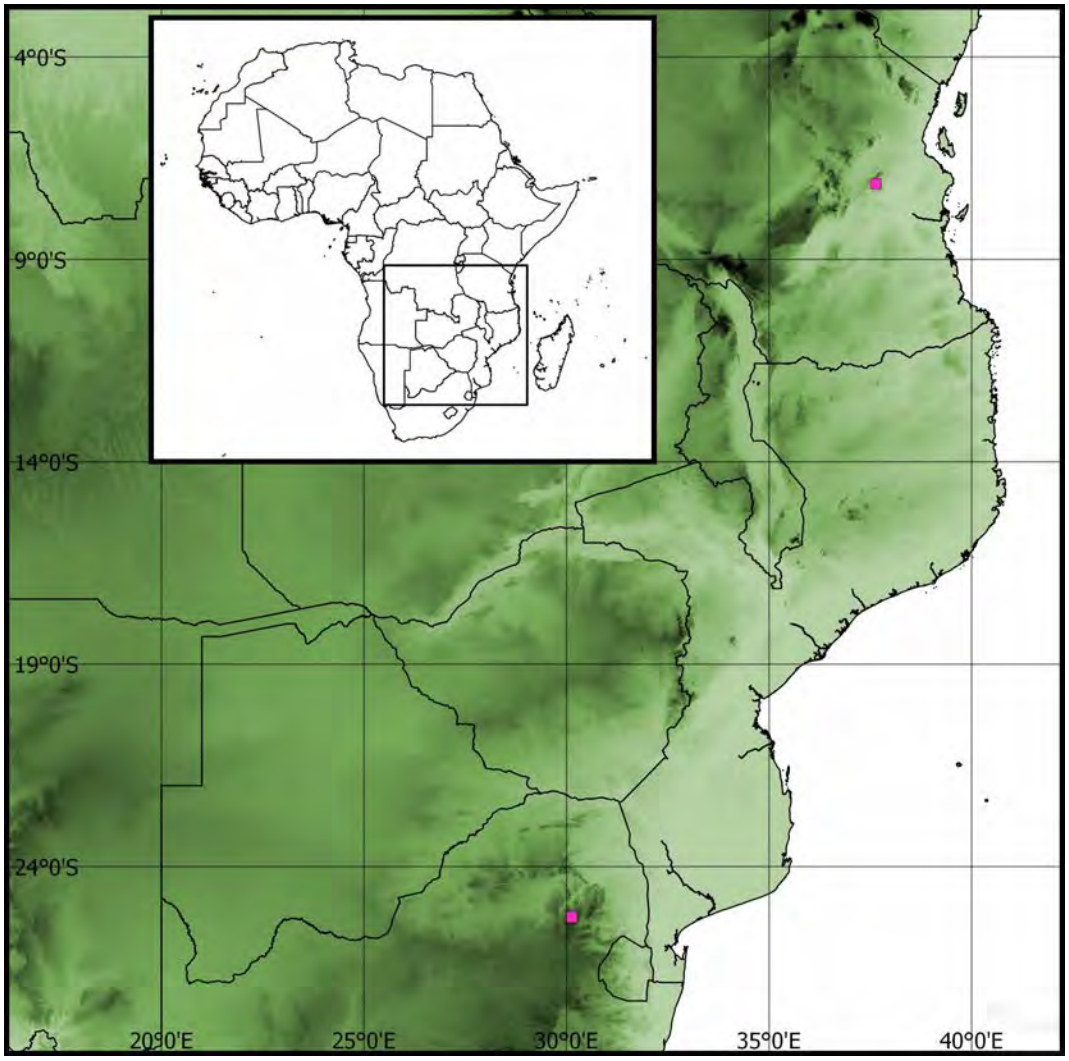

Figure 5.30: Distribution of *E. zygolimbatus* in Africa.

Note

The species can be confused with *E. curvipes*, see Note under that species.

Specimens Examined

TANZANIA. Morogoro District. South Uluguru Mts., in gorge of Mgeta River Falls at east edge of Lukwangule Plateau, *T. Pócs, R. Ochyra & H. Bednarek–Ochyra*

88108/M, 9/6/1988 (BOL, E, EGR, MO, PRE, S(B174704)).

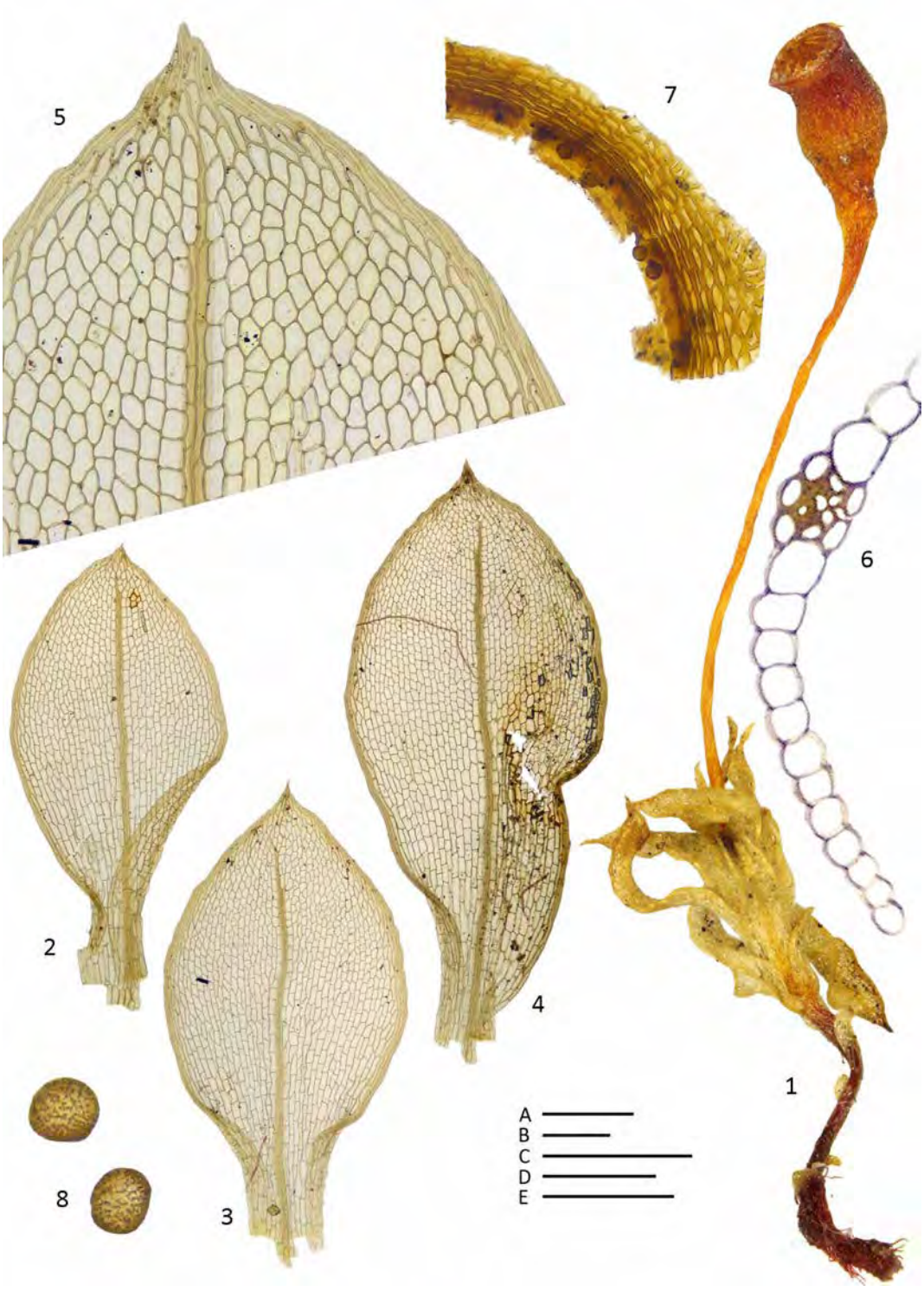

Figure 5.31: *Entosthodon zygolimbatus.* 1. Habit, dry; 2–4. Leaves; 5. Leaf apex; 6. Leaf cross-section; 7. Capsule mouth & peristome; 8. Spores. All from: *T. Pócs, R. Ochyra & H. Bednarek–Ochyra 88108/M*, BOL. Scale bars: A (2–4) = 500 µm; B (5, 7) = 100 µm; C (1) = 1 mm; D (6) = 100 µm; E (8) = 50 µm.

5.4.4. *Fifeobryum* N. Wilding

Fifeobryum N. Wilding, Chapter 2.–TYPE: *Fifeobryum longicollis* (Dixon) N. Wilding, Chapter 2.

Plants medium, gregarious, dark green. Stems reddish–brown, to 6 mm, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled, reddish cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. Leaves erect–spreading, contorted when dry, strongly keeled, oblong-obovate to spathulate, 2.5–4.6 x 1–1.9 mm, short–acuminate to apiculate, margins weakly to strongly toothed in upper ½–⅓ by, usually obtuse, projecting cells, aristate; cells of upper lamina thin walled, quadrate to hexagonal or oblong–hexagonal, 37–50(58) x (15)20–30 µm; basal cells rectangular, thinner-walled (37)62–150(213) x 27–38(50) µm; marginal cells undifferentiated; costae percurrent to short excurrent-aristate, arista to 200 µm, in cross-section with two adaxial and one abaxial layer of large cells surrounding a central stereid group. Axillary-hairs present, hyaline, multicellular, uniseriate, the apical cell largest and with rounded end walls. Polyoicous. Perigonia single, terminating primary shoot, synoicous shoots arising by sub–perigonial innovation. Paraphyses club–shaped. Setae 3–8 mm long, pale–yellow to reddish–brown, twisted anti–clockwise, smooth, straight or slightly curved. Capsules erect to weakly inclined, zygomorphic, oblong–pyriform, 1.5–2.8 x 0.3–0.7 mm, yellow to reddish–brown at maturity, constricted below mouth when dry, with a well differentiated neck *ca*. ½ the total length of the capsule, neck sulcate; mouth *ca*. ¾ the diameter of the capsule, slightly oblique; exothecial cells with obscure lumina, (30)50–78 x 10–20(25) µm, pentagonal to oblong-hexagonal, in cross-

section with thick, strongly cuneate anticlinal walls, 3–5 rows of oblate cells at mouth. Opercula plano–convex to short–conic, cells not or slightly twisted anti–clockwise from above. Peristome absent or single, fugacious; exostome teeth rudimentary or absent, irregular in shape, pale-orange, to 35 µm high, *ca*. 28 µm wide at base, apices not connected, papillose. Spores tetrahedral, 27–35 µm, finely papillose to verrucate–lirate or reticulate, trilete scars often visible. Calyptrae cucullate, rostrate.

The genus comprises three species with austral distributions. One species occurs in sub-Saharan Africa, *F. longicollis*, with an additional species in each of Australia (*F. smithhurstii*) and South America (*F. balansae*), see Chapter 2.5. The bulging, toothed marginal cells and robust often dark green plants unite species of the genus.

Fifeobryum longicollis (Dixon) Wilding, Chapter 2. *Funaria longicollis* Dixon, S. African J. Sci. 18: 318 (1922). *Entosthodon dixonii* Sim, Bryoph. S. Afr. 296 (1926), non *E. longicollis* Mitt. (1869).–TYPE: ZIMBABWE. Zimbabwe Ruins, 3000 ft, *Sim 8735*, July 1920 (BM, lectotype!, designated here; isolectotypes in BOL!, PRE!). I have chosen a type specimen from BM, one of four listed by Dixon in the protologue, to serve as the lectotype because Dixon's herbarium is housed at BM and *Sim 8735* contains good material.

Synonyms:

Funaria decaryi Thér., Recueil Publ. Soc. Havraise Études Diverses 1926: 47. ic. 1927.–TYPE: MADAGASCAR. Ambovombe, "sur sable crystalline", *Decary s.n.* (PC (PC0134310), lectotype!, designated here; isolectotypes in PC! (PC0134310 & PC0134311); S!: (B118700 & B118701)). I have chosen a PC collection to serve as the lectotype because it is the location of the authors herbarium, the collection is in good condition and closely fits Thériot's description of the species.

Entosthodon kadzianus Rehmann, nom. nud., Bull. Misc. Inform. Kew 1923: 203 (1923).

Illustration : Figure 5.33.

Plants medium, dark green. *Stems* reddish–brown, to 6 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. *Leaves* erect–spreading, oblong–obovate to spathulate, 2.5–4.6 x 1–1.9 mm, concave, strongly keeled, short–acuminate to apiculate, weakly to strongly toothed in upper ½–⅓ by, usually obtuse, projecting cells, aristate, arista to 200 µm;

cells of upper lamina quadrate to hexagonal or oblong–hexagonal 37–50(58) x (15)20–30 µm; *basal* (37)62–150(213) x 27–38(50) µm; *marginal cells* undifferentiated; *costae* percurrent to short excurrent.

Polyoicous. *Setae* 3–8 mm long, straight or slightly curved, smooth, pale–yellow to reddish–brown, twisted anti–clockwise. *Capsules* erect to weakly inclined, zygomorphic, oblong–pyriform, 1.5–2.8 x 0.3–0.7 mm, constricted below mouth when dry, yellow to reddish–brown at maturity, with a well differentiated neck *ca*. ½ total length of capsule; *mouth* slightly oblique, *ca.* ¾ diameter of capsule; *exothecial cells*, (30)50–78 x 10–20(25) µm, in cross-section with thick, strongly cuneate anticlinal walls, *ca*. 3–5 rows of oblate cells at mouth. *Operculum* plano–convex to short–conic, cells not or slightly twisted anti–clockwise from above. *Peristome* absent or single and rudimentary; *exostome teeth* straight, irregular in shape, rudimentary, pale orange, apices rounded, to 35 µm high, *ca*. 28 µm wide at base, papillose. *Spores* 27–35 µm, tetrahedral, finely papillose to verrucate–lirate or reticulate, trilete scars often visible. *Calyptrae* cucullate, rostrate.

Diagnostic Features

The conspicuous teeth on the margins of the leaf make *F. longicollis* easy to identify. Less dentate forms of the species could conceivably be confused with *Funariella campylopodioides*, however the latter lacks a peristome and has verrucate–bacullate spores.

Habitat and Distribution

Fifeobryum longicollis is known from the northern parts of South Africa and the southern parts of Botswana, Zimbabwe, and Madagascar (Figure 5.32). It is recorded from elevations between 600 m and 1500 m.

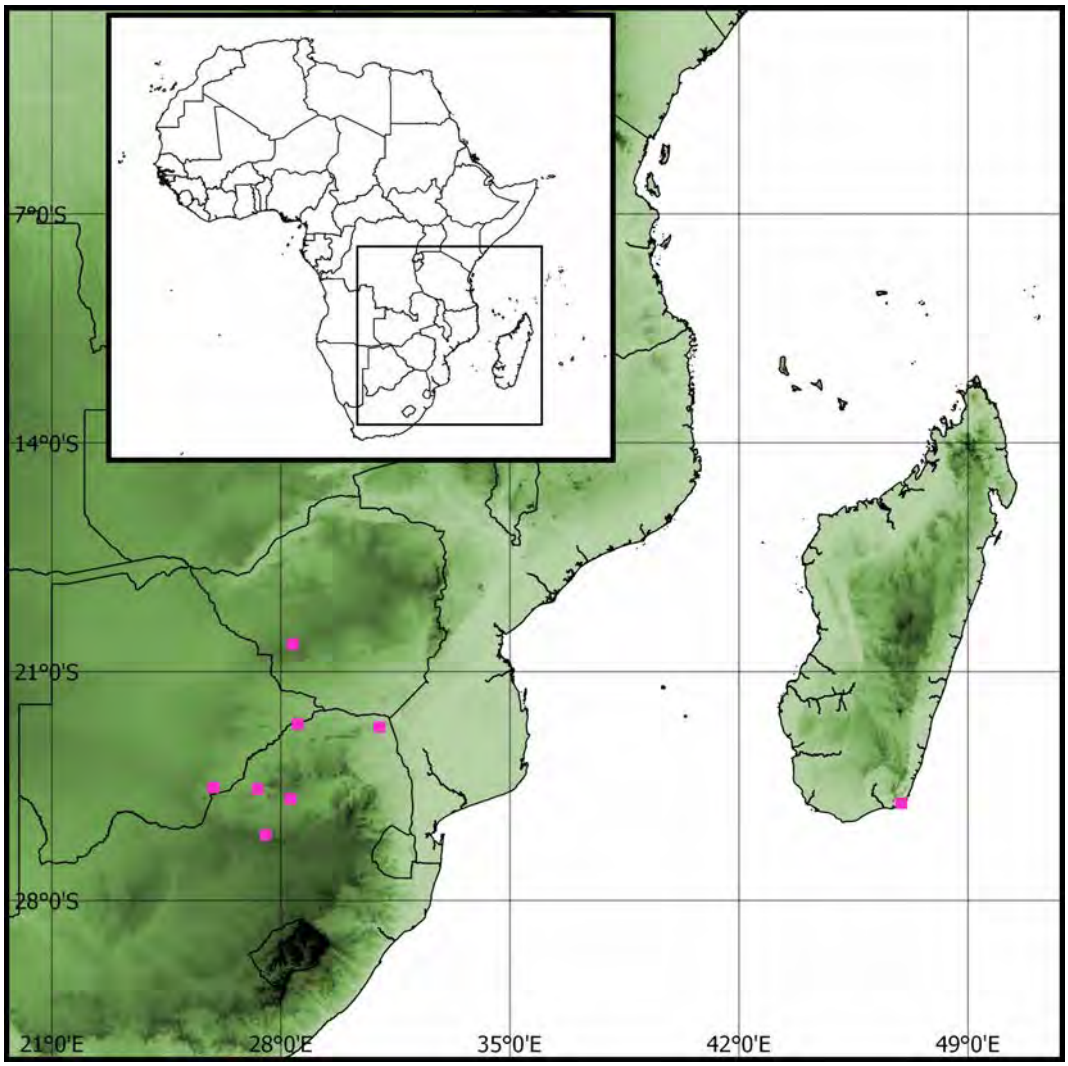

Figure 5.32: Distribution of *F. longicollis* in Africa.

Note

In the few Madagascan specimens that I have studied the spores have a different ornamentation (verrucate lirate and finely papillose when immature), basal cells are smaller on average than the Southern African material and the leaves are more strongly toothed. Based on my observations of other members of the family, I consider this normal intraspecific variation for a species, especially given the

significant disjunction between the continental and island populations.

Specimens Examined

BOTSWANA. South East District, *O.J. Hansen 3308*, 19/12/1978 (PRE, MO).

MADAGASCAR. Fort Dauphin, *Decary 11*, 20/6/1926 *38*, 9/7/1926, *40*, 2/7/1926 (MO).

SOUTH AFRICA. Gauteng, Magaliesberg, *J. Van Rooy 613*, x/5/1980 (PRE, MO), *621*, x/5/1980 (MO); Limpopo, Klein Kariba, *S.M. Perold 51*, 1/8/1981 (PRE, MO), *S.M. Perold 45*, 1/8/1981 (PRE); *Punda Milia, R.E. Magill 5018*, 23/2/1978 (MO); Thabazimbi, *L. Smook 3184*, 15/3/1981 (PRE), *3185*, 15/3/1981 (PRE, MO); Kruger N.P., *R.E. Magill 5018*, 23/2/1978 (PRE); Matoppos, *H.A. Wager 1503* (PRE).

ZIMBABWE. Zimbabwe Acropolis, *Sim 8796*, x/7/1920 (BOL, PRE); Near native church, *Sim 8797*, x/7/1920 (BOL, PRE); Khami Ruins, *Sim 8842*, x/7/1920 (BOL, PRE); Matoppos Mts., *Wager 900*, x/x/1920 (BOL).

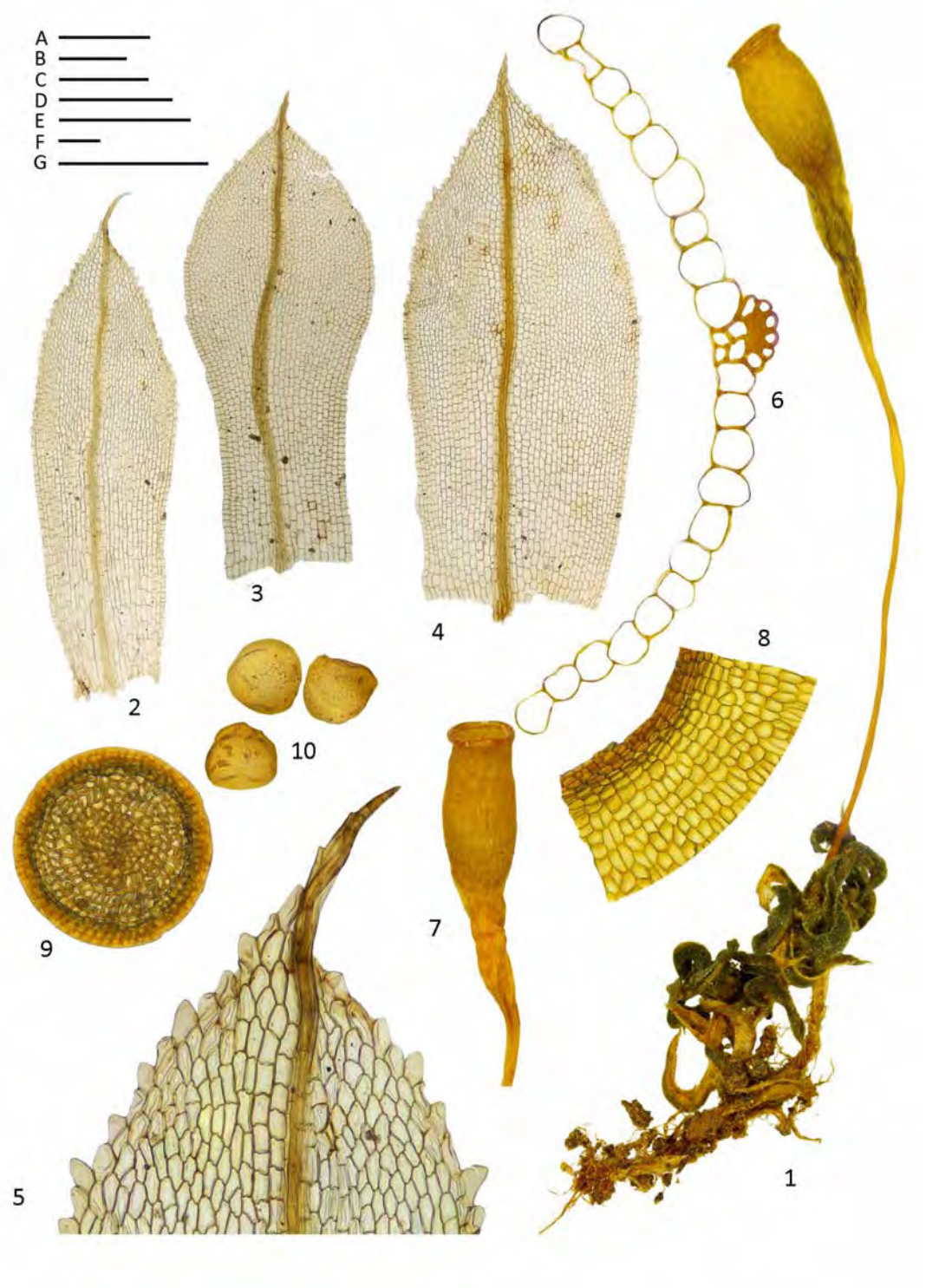

Figure 5.33: *Fifeobryum longicollis.* 1. Habit, dry (*R.E. Magill 5018*, PRE); 2–4. Leaves (2 – *Decary 11*, MO; 3 – *Smook 3185*, PRE, MO; 4 – *Decary 38*, MO); 5. Leaf apex (as for 2); 6. Leaf cross-section (as for 3); 7. Capsule, dry (as for 3); 8. Capsule mouth & exothecial cells (*Decary s.n.*, MO); Operculum (as for 2); Spores (as for 3). Scale bars: A (2–4) = 500 µm; B (5, 8) = 100 µm; C (1) = 1 mm; D (6) = 100 µm; E (10) = 50 µm; F (9) = 100 µm; G (7) = 1 mm.

5.4.5. *Funariella* Sérgio

Funariella Sérgio, Orsis 3: 10. 1988.–TYPE: *Funariella curviseta* (Schwägr.) Sérgio, Orsis 3: 10 (1988).

Synonyms:

Entosthodon sect. Plagiocleidion Müll. Hal., Gen. Musc. Fr. 107. 1900. *Funaria sect. Plagiocleidion* (Müll. Hal.) Broth., Nat. Pflanzenfam. [Engler & Prantl] I(3): 522. 1903.–TYPE: *Entosthodon curvisetus* (Schwägr.) Müll. Hal.

Funaria sect. Plagiodus Mitt., J. Linn. Soc., Bot. 12: 248. 1869. *Entosthodon subg. Plagiodus* (Mitt.) Fife, J. Hattori Bot. Lab. 58: 191. 1985.–LECTOTYPE (designated by Fife (1985)): *Funaria laevis* Mitt.

Plants small to large, gregarious, pale green to dark green. Stems reddish-brown or orange-brown, to 25 mm, branched at least once by sub-perigonial innovation, in cross-section with 1–3 layers of thick-walled, reddish cortical cells, a hyalodermis and a central strand, rhizoids reddish-brown. Leaves erect–spreading, little contorted to contorted when dry, 1.1–3(5.2) x 0.4–1.9 mm, concave, strongly keeled, or plane, ovate, obovate, elliptical, oblong–obovate, spathulate, rarely lingulate or ligulate, usually short acuminate, less frequently apiculate, margins toothed in upper-half by projecting cells or entire, arista present or absent; cells of upper lamina, thin-walled, quadrate or rhomboidal to oblong-hexagonal, (16)30–75(88) x (8)17–38 µm, often irregularly arranged; basal cells rectangular, thinner-walled, longer and laxer, (25)50–188(225) x (17)25–44(75) µm; marginal cells narrower and forming a border 1–2 cells wide in the upper ⅓ or undifferentiated; costae ending well below apex to excurrent-aristate, in cross-section with two adaxial

and one abaxial layer of large cells surrounding a central stereid group. Axillary-hairs present, hyaline, multicellular, uniseriate, the apical cell largest and with rounded end walls. Polyoicous. Perigonia single, terminating primary shoot, synoicous shoot arising by sub-perigonial innovation. Paraphyses club-shaped. Setae to 15 mm long, pale-yellow to reddish-brown, usually twisted anti-clockwise, rarely twisted clockwise, smooth, straight to curved, polysetae rare. Capsules erect or inclined, radially symmetric or zygomorphic, gibbous, oblong-pyriform, oblong-obovoid, narrowly oblong-obovoid, 0.9–4 x 0.3–1.5 mm, usually reddish-brown at maturity, constricted below the mouth when dry, with neck ¼–½ the length of the capsule, neck sulcate; mouth ⅔ to equal the diameter of the capsule, transverse or oblique; exothecial cells with obscure lumina, 20–85(108) x 10–28 µm, oblong hexagonal to pentagonal, in cross-section with cuneate anticlinal walls, 2–8 rows of oblate cells at mouth. Opercula plane, plano–convex, rarely short-conic, cells not twisted or twisted anti-clockwise from above. Peristome double, single or absent, fugacious; exostome teeth well developed, rudimentary or absent, regular or irregular in shape, straight or sigmoidal, 150–330 high x 22–88 µm, apices not connected, not or weakly appendiculate, papillose, striate, adaxial surface trabeculate; endostome segments well-developed, rudimentary or absent, papillose, joined at base, 20–180 x 25–100 µm. Spores tetrahedral, (22) 25–38 µm, collapsed or retaining shape, verrucate-lirate, verrucate-bacullate, bacullate-insulate, minutely-verrucate, smooth, finely-papillose, rarely reticulate or lirate-bacullate; trilete scar present or absent. Calyptrae, cucullate, rostrate.

Funariella was originally decribed by Sérgio (1988) to accommodate the Mediterranean species *Entosthodon curvisetus* (Schwägr.) Müll.Häl. which she believed to be unique among other members of the genus and family. Sérgio (1988) considered differences in spore ornamentation and length of the seta among other

characters to warrant placement in its genus. Recent work (chapters 2-5), however, has shown that *F. curviseta* is neither morphologically nor genetically particularly distinct from other members of *Entosthodon s.l.*. Therefore, the genus is here expanded to included additional, phylogenetically closely related species. The genus comprises 9 species in Africa and at least 4 from outside of Africa (Chapters 2, 4). *Funariella curviseta* is the only Northern Hemisphere species in the genus.

Funariella campylopodioides (Müll. Hal.) N. Wilding, Chapter 2. *Entosthodon campylopodioides* Müll. Hal., Hedwigia 38: 60. 1899. *Funaria campylopodioides* (Müll. Hal.) Broth., Nat. Pflanzenfam. [Engler & Prantl] I(3): 525 (1903).–TYPE: SOUTH AFRICA. Free State ("Orange Freistaat"), Taaibosch Kranz, Renoster river, *A. Rehmann s.n.*, 18/5/1880 (S, lectotype!(B77399), designated here; isolectotype in G!). Müller's type specimen was presumably destroyed in the Allied bombing of Berlin during WWII. A duplicate of Rehmann's collection from S fits Müller's description of the species well and is here chosen to serve as the lectotype.

Synonyms:

Entosthodon chlorophyllosus Rehmann, nom. nud., Index Bryol. 422 (1896). (BM). Illustration: Figure 5.35.

Plants medium, light–green. *Stems* orangish–brown, to 5 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. *Leaves* erect–spreading, contorted when dry, elliptical to obovate or spathulate, (2)2.5–3(3.5) x 0.8–1.6(1.9), mm, plane to concave, short–acuminate to apiculate, weakly toothed or entire, aristate, arista to 360 µm; *cells of upper lamina* rhomboidal to hexagonal or oblong–hexagonal, (25)37–50(63) x 17–28(35) µm; *basal* (32)55–113 x (20)26–43(58) µm; *marginal cells* undifferentiated, or in some populations bulging outwards in upper ⅓; *costae* mostly excurrent, less often percurrent.

Polyoicous. *Setae* 2.5–6 mm long, straight to slightly curved near base of capsule, pale–yellow to reddish–brown, twisted anti–clockwise. *Capsules* inclined to horizontal, zygomorphic, oblong-obovoid, (1.5)2–3(3.5) x (0.5)0.7–1 mm, con-

stricted below mouth when dry, yellow to reddish–brown at maturity, with a well differentiated neck *ca*. ½ total length of capsule; *mouth* slightly oblique, *ca*. ¾ diameter of capsule, flaring in older capsules; *exothecial cells* (30)50–75(85) x (10)12–20(23) µm, in cross-section with thick, strongly cuneate anticlinal walls (30)50–75(85) x (10)12–20(23) µm, 4–8 rows of oblate cells at mouth; *opercula* plano–convex, cells not twisted. *Peristome* absent. *Spores* 25–30 µm, tetrahedral, verrucate to bacullate, rarely lirate–baculate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Funariella campylopodioides can be recognized by its combination of eperistomate, clavate capsules and elliptical to obovate or spathulate leaves. The species can be confused with *F. urceolata*, as both share oblong–pyriform capsules, *F. urceolata*, however, differs by having lingulate to oblong–obovate leaves, which can be up to twice as large. *F. urceolata* can be peristomate, which can further aid in differentiating the two. Less dentate forms of *Fifeobryum longicollis* can also be confused with *F. campylopodioides* (see Note under *F. longicollis*).

Habitat and Distribution

Funariella campylopodioides occurs in open grassland and shrubland of the northern, eastern and southern parts of South Africa (Figure 5.34) at elevations between 1000 m and 1700 m.

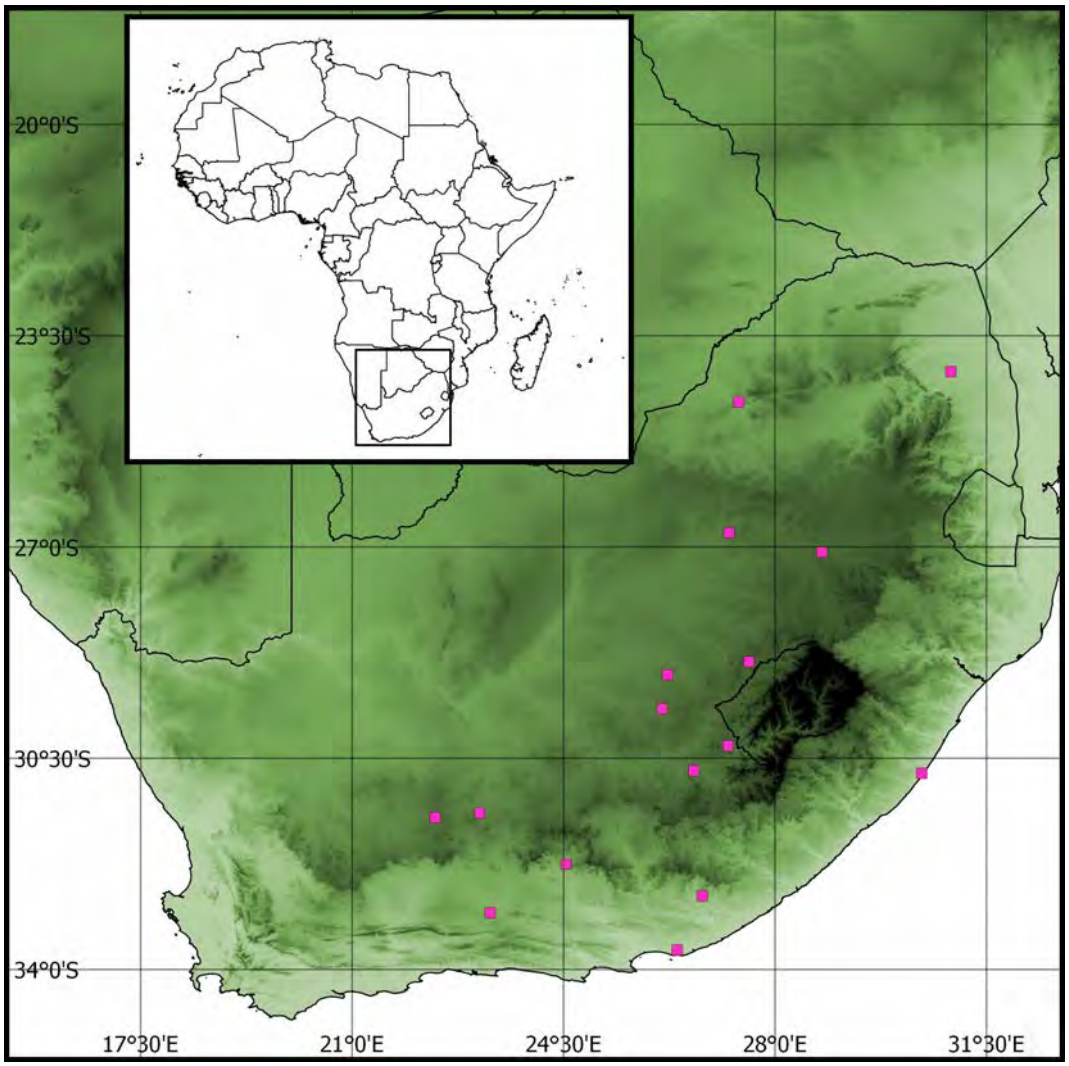

Figure 5.34: Distribution of *F. campylopodioides* in Africa.

Note

The south Asian name *E. rottleri* (Schwägr.) Müll. Hal. has long been applied to this African species. Müller (1849) reported *E. rottleri* as being 'non–raro' in the Cape of South Africa. Based on morphology, *E. rottleri* is, without doubt, a close relative of *F. campylopodioides*. It differs, however, in having carinate leaves that are more acuminate, and margins that are toothed near the apex of the

leaf, similar to those of *Fifeobryum longicollis*, which according to phylogenetic data is a close relative of *F. campylopodioides* (Chapter 2).

Specimens Examined

SOUTH AFRICA. Eastern Cape: Graaf–Reinet, *N. Wilding 238*, 27/4/2013 (BOL); Dekselfontein, *S.M. Perold 4225*, 12/10/1999 (PRE, MO); Victoria East, *Farqukar 79*, 1/5/1911 (PRE), *N. Wilding 244*, 29/4/2013 (BOL); Port St. Johns, *H.A. Wager 1460* (PRE); Rietbron, *S.M. Perold 4784*, 24/9/2003 (PRE); Free–State: Bloemfontein, P*rof. Potts s.n.,* 1/5/1917 (PRE); *E.A. Schelpe s.n.,* 1/10/1963 (BOL) , *O.H. Volk* 18/2/85, 13/4/1981 (MO); Elandsberg, *J. Van Rooy 2404*, 1/2/1986, 2428, 1/2/1986 (PRE, MO), *2447*, 1/2/1986 (PRE), *2456*, 1/2/1986 (PRE, MO); Aliwal North, *L. Smook 2990*, 3/3/1981 (MO); Clocolan, *J. Van Rooy 509*, 1/2/1980 (PRE, MO); Reddersburg, *J. Van Rooy 2350*, 1/2/1986 (PRE); Parys, *N.V. Kroon 16309*, 7/12/2000 (PRE); Limpopo: Bakkers Pass, *Hard, Retief & Herman 5338a, 5339a*, 26/3/1980 (MO); Pepeti falls, *P. Thomas 2958*, 30/4/1931 (MO); Thabazimbi, *S.M. Perold 851*, 6//1985 (PRE, MO), *853*, 6/3/1985 (PRE); Mpumalanga: *D.F. Chaludy s.n* (S:B100459); Lydenburg, *R.E. Magill 3135*, 31/1/1977 (PRE); Northern Cape: Loxton, *T.A.J. Hedderson 16971*, 2/4/2009 (BOL); Victoria West, *T.A.J. Hedderson 16954, 16959,* 1/4/2009 (BOL).

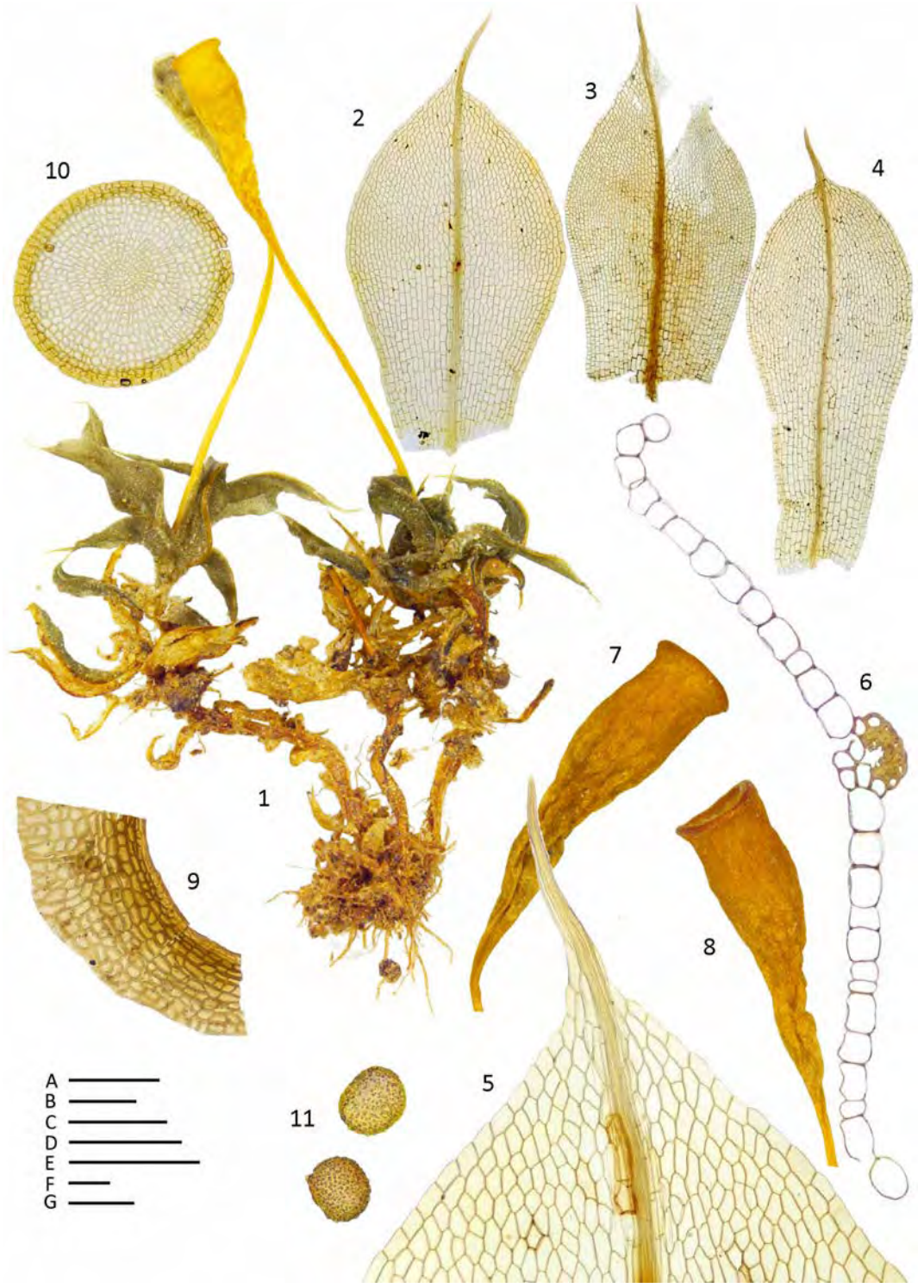

Figure 5.35: *Funariella campylopodioides*. 1. Habit, dry (*S.M. Perold 851*, PRE); 2–4. Leaves (2 – *N. Wilding 238*, BOL; 3 – *T.A.J. Hedderson 16954*, BOL; 4 – *N.V. Kroon 16309*, PRE); 5. Leaf apex (as for 2); 6. Leaf cross-section (as for 3); 7, 8. Capsule, dry (*Hard, Retief & Herman 5338a*); 9. Capsule mouth & exothecial cells (*H.A. Wager 1460*, PRE); 10. Operculum (as for 1); 11. Spores (as for 2). Scale bars: A (2–4) = 500 µm; B (5, 9) = 100 µm; C (1) = 1 mm; D (6) = 100 µm; E (11) = 50 µm; F (10) = 100 µm; G (7, 8) = 1 mm.

Funariella chevalieri (P. de la Varde) N. Wilding comb. nov. Basionym: *Funaria chevalieri* P.de la Varde, Bull. Mus. Natl. Hist. Nat. 15: 242. 4 (1943).–TYPE: CAPE VERDE, FOGO. Curral Chupadeiro, sources, *G. Chevalier s.n.*, 26 July 1934. (PC, holotype! (PC106750); isotypes in PC (PC106748! & PC106749!)).

Illustration: Figure 5.37.

Plants small, light–green. *Stems* reddish–brown, to 3 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids orange or reddish–brown. *Leaves* erect–spreading, little contorted when dry, ovate to oblong–obovate, 1.1–2.6 x 0.4–0.7 mm, concave, short acuminate, entire, aristate, arista to 250 µm; *cells of upper lamina* quadrate or rhomboidal to oblong–hexagonal, 45–53 x 15–20 µm; *basal* (40)50–75 x 17–30 µm; *marginal cells* undifferentiated; *costae* ending below apex.

Polyoicous. *Setae* 2.5–6 mm long, straight to curved, pale–yellow to reddish–brown, twisted anti–clockwise. *Capsules* horizontal, gibbous, zygomorphic, oblong-obovoid, 0.9–1.5 x 0.3–0.5 mm, constricted below mouth when dry, yellow to reddish-brown at maturity, with a well differentiated neck *ca*. ½ total length of capsule; *mouth* slightly oblique, *ca*. ¾ diameter of capsule; *exothecial cells*, 25–40 x 10–25 µm, in cross-section with thick, strongly cuneate anticlinal walls, 2–4 rows of oblate cells at mouth. *Opercula* not seen. *Peristome* double; *exostome teeth* straight to sigmoidal, orange, to 213 µm high, *ca*. 50 µm wide at base, striate, trabeculate; *endostome teeth* straight, hyaline, to 100 µm high and 63 µm wide. *Spores* 25–30 µm, tetrahedral, collapsed, smooth to minutely verrucose. *Calyptrae* not seen.

Diagnostic Features

Among the African species *F. chevalieri* can be confused with *F. sulcata* as both species share aristate, short–acuminate leaves and peristomate, zygomorphic capsules. *Funariella chevalieri* can be distinguished by its spores, which are generally larger than those of *F. sulcata* (13–23 µm) and by the absence of elongated marginal cells, which in *F. sulcata* are usually present in the upper third of the leaves.

The ornamentation and shape of the peristome teeth, in *F. chevalieri*, remain obscure because of a lack of capsules with intact peristomes in the type material.

Habitat and Distribution

The species is known only from the original collection on Fogo Island, Cape Verde (Figure 5.36). No information about the habitat is provided in either the description or with the original collections.

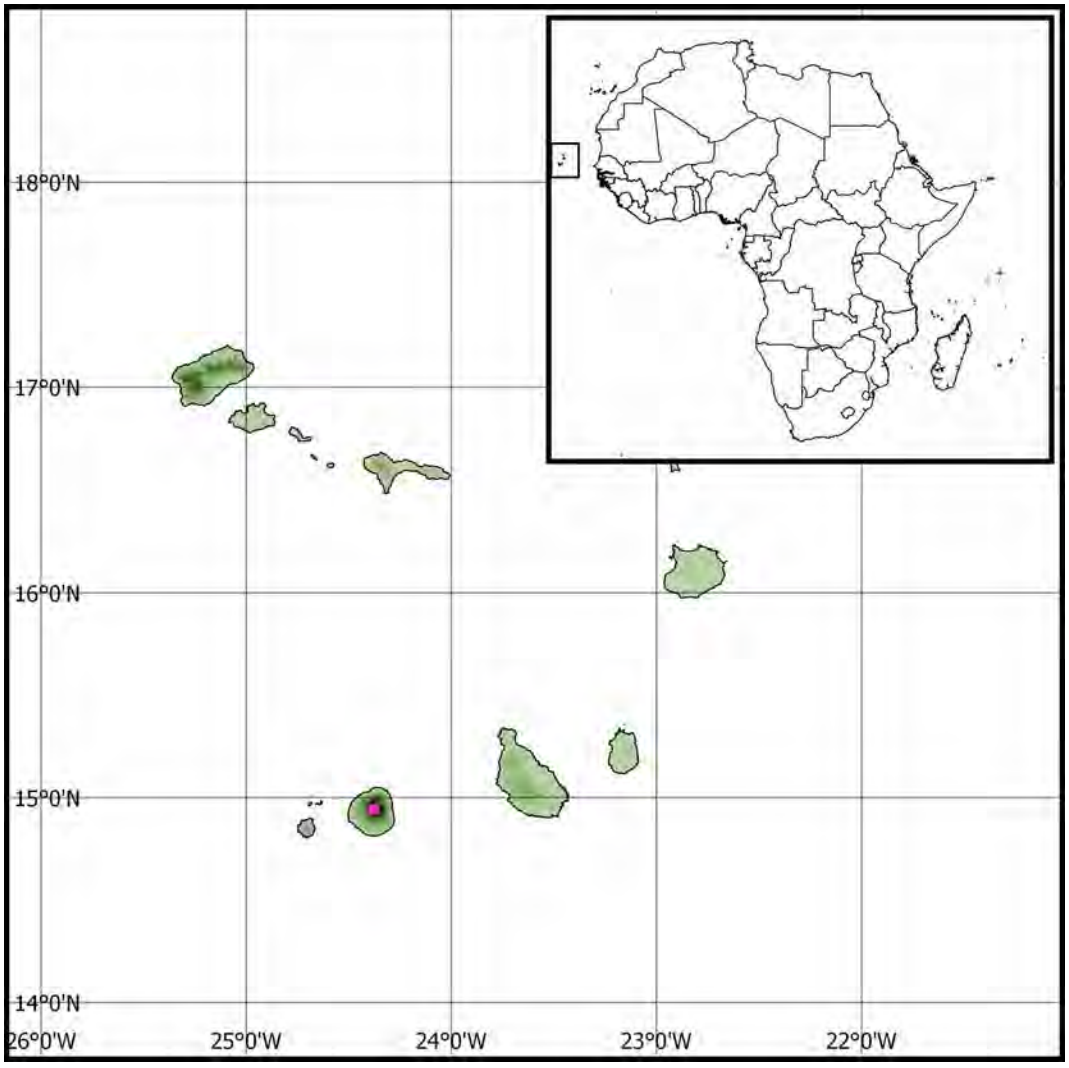

Figure 5.36: Distribution of *F. chevalieri* in Africa.

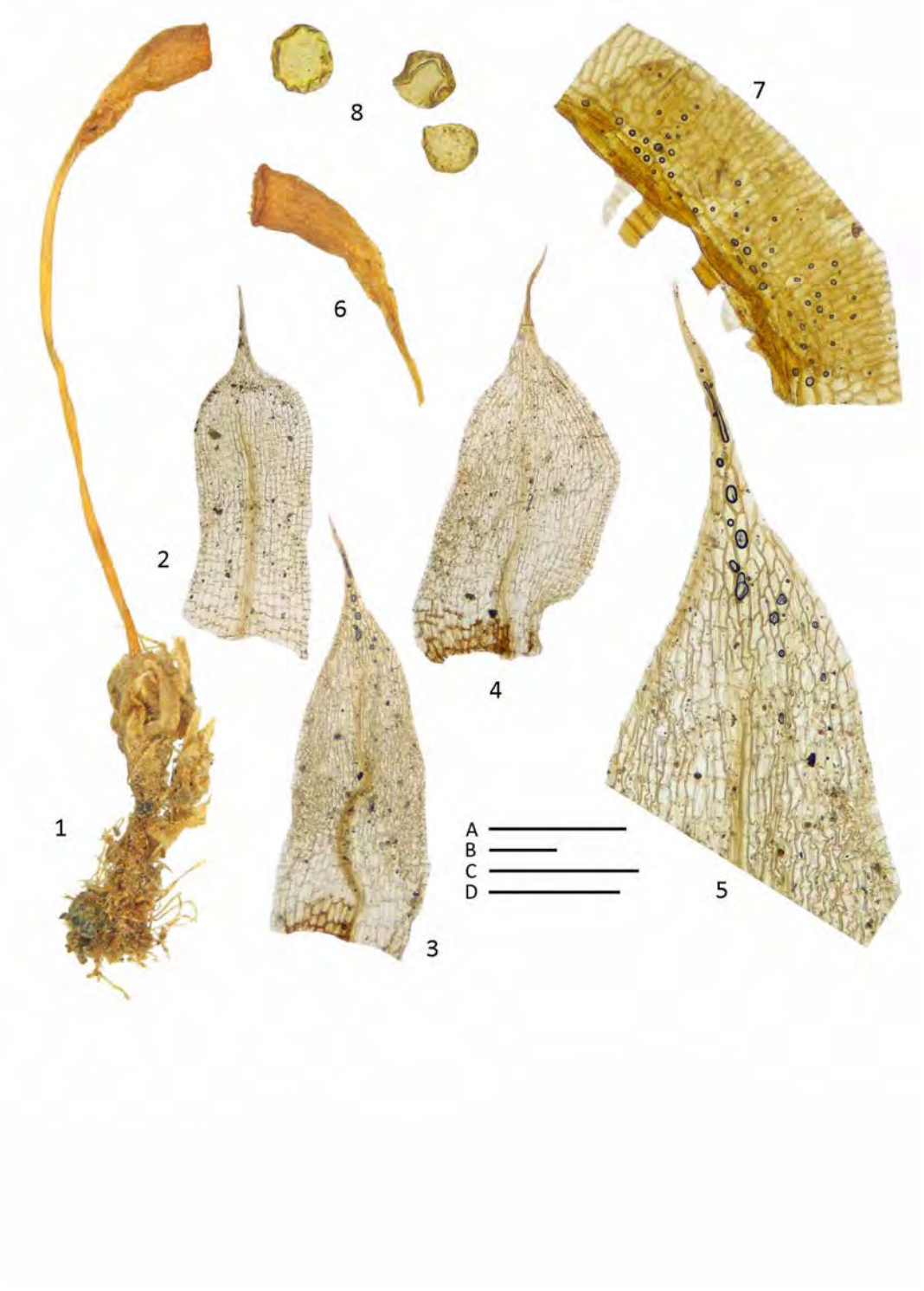

Figure 5.37: *Funariella chevalieri.* 1. Habit, dry; 2–4. Leaves; 5. Leaf apex; 6. Capsule, dry; 7. Capsule mouth & peristome; 8. Spores. All from : *G. Chevalier s.n.* (PC0106749), PC. Scale bars: A (2–4) = 500 µm; B (5, 7) = 100 µm; C (1, 6) = 1 mm; D (8) = 50 µm.

Funariella clavata (Mitt.) N. Wilding, Chapter 2. *Entosthodon clavatus* Mitt., Thes. Cap. 1:63 (1859). *Funaria clavata* (Mitt.) Magill, Fl. S. Africa, Bryophyta 2: 326 (1987).–TYPE: SOUTH AFRICA. Cape of Good Hope, *Menzies s.n.* (NY, holotype!).

Illustration: Figure 5.39.

Plants small, light–green. *Stems* reddish–brown, to 5 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. *Leaves* erect–spreading, little contorted when dry, ovate to obovate or orbicular, 1.8–2.8 x 0.8–1.7 mm (including arista), plane to concave, entire, gradually apiculate to aristate, arista to 300 µm; *cells of upper lamina* quadrate or rhomboidal to oblong–hexagonal, 30–55 (63) x 12–25(30) µm, *basal* (38)57–138(163) x (23)28–45(60) µm; *marginal cells* undifferentiated; *costae* usually ending below apex, sometimes extending into apex and fusing with arista.

Polyoicous. *Setae* 2–5 mm long, curved near base of capsule, yellow to reddish–brown, twisted anti-clockwise. *Capsules* inclined to horizontal, radially symmetric, narrowly oblong-obovoid, 1.5–4 x 0.6–1.5 mm, weakly constricted below mouth when dry, yellowish to brown at maturity, with a well differentiated neck *ca*. ⅓–½ total length of capsule; *mouth* transverse, *ca*. ¾ diameter of capsule; *exothecial cells* 50–108 x 15–28 µm, in cross-section with thick, strongly cuneate anticlinal walls, 2–3 rows of oblate cells at mouth. *Opercula* plane, cells not twisted. *Peristome* usually absent, if present consisting of a highly reduced and fragmented hyaline membrane. *Spores* 27.5–35 µm, tetrahedral, usually collapsed, finely verrucose, trilete scars visible. *Calyptrae* cucullate, rostrate.

Diagnostic Features

The species is easily recognizable by its clavate, eperistomate capsules.

Habitat and Distribution

Funariella clavata is endemic to the winter rainfall region of South Africa (Figure 5.38). It is found in shrubland of the Western and Northern Cape, at elevations below 1300 m. *Funariella clavata* can be observed in fairly arid situations and on fairly coarse sandy soils, exposed embankments and around the base of low shrubs.

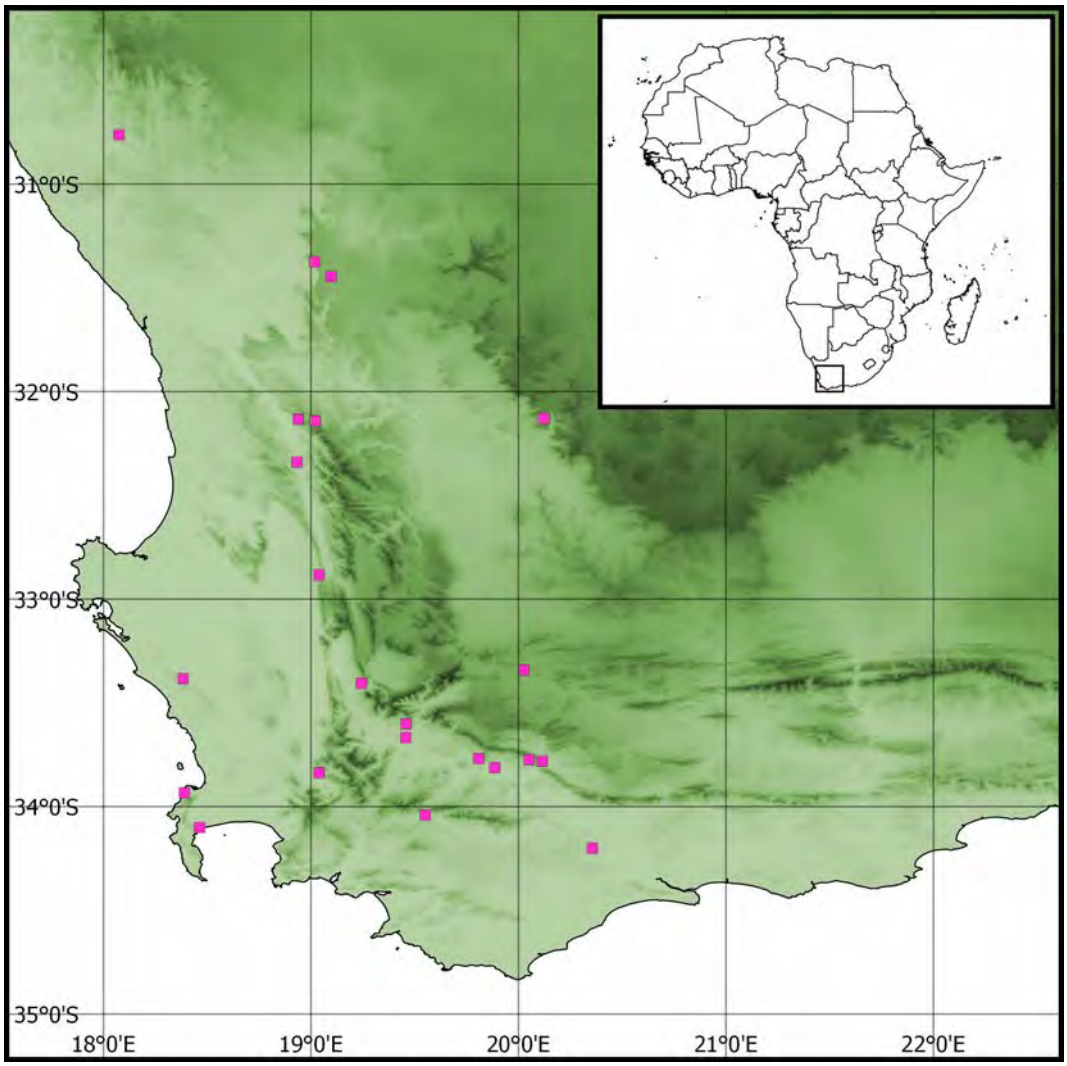

Figure 5.38: Distribution of *F. clavata* in Africa.

Note

Funariella clavata shares an overall likeness with the Australian *Funariella apophysatus* (Taylor) N. Wilding and South American *Funariella chilensis* (Thér.) N. Wilding. The three species are phylogenetically closely related (Chapter 2) and Fife (1982) previously commented that the Australian and South American species may be synonymous. The species has a tendency to produce multiple setae per

sporophyte.

Representative specimens

SOUTH AFRICA. Western Cape: Ashton, *N. Wilding 226*, 9/10/2012, *210*, 21/10/2011 (BOL); Cape Town, *Rehmann 179*, 1875–1877 (BOL, S), *N. Wilding 210* (BOL), *S.Arnell 54*, 30/8/1951 (S), *1178*, 28/10/1951 (S); *Breutel s.n*. (S); *R.E. Magill & E.A. Schelpe 4090*, 18/8/1977 (MO); Touws River, *T.A.J. Hedderson 17741*, 5/9/2011 (BOL), *N. Wilding HBCT303a, 303b, 309*, 5/9/2011 (BOL); Citrusdal, *K.H. Barnard 49653*, 1/9/1931 (PRE); Clanwilliam, *N. Wilding 211* (BOL), *R.E. Magill & E.A. Schelpe 4003*, 14/8/1977 (MO), 4030a, 14/8/1977 (PRE, MO); *T.A.J. 14316*, 5/10/2001; *Darling, S.M. Perold 481*, 9/10/1984 (MO); Franschoek, *N. Wilding 249*, 10/10/2012 (BOL); Montagu, *S. Arnell 724*, 18/9/1951 (S), *784*, 19/9/1951 (S), *838*, 20/9/1951 (S); *N. Wilding 227, 246, 254*, 8/10/2012 (BOL); Porterville, *T.A.J. Hedderson 13983*, 23/6/2001 (BOL); Robertson, *T.A.J. Hedderson 16854*, 30/8/2008, *16861*, 30/8/2008, *16864* (BOL); Swellendam, *T.A.J. Hedderson 16444* (BOL); Tulbagh, *N. Wilding 234*, 2/11/2012 (BOL); Worcester, *T.A.J. Hedderson 16877b*, 31/8/2008 (BOL), *I.M. Wilman 1088*, 13/9/1951 (PRE); Nuy Valley, *N. Wilding 248*, 9/10/2012 (BOL); Northern Cape: Cederberg Wilderness Area, *T.A.J. Hedderson 14316* (BOL); Nieuwoudtville, *N. Wilding 250*, 1/8/2011 (BOL), *R.E. Magill & E.A. Schelpe 3926*, 13/8/1977 (PRE, MO); Tankwa Karoo National Park, *T.A.J. Hedderson 17124*, 10/9/2010 (BOL), *S.P. Bester 7079*, 5/8/2006 (PRE); Olienpoort, *Van Der Westhuizen & Deetlefs 40*, 1/11/1977 (PRE).

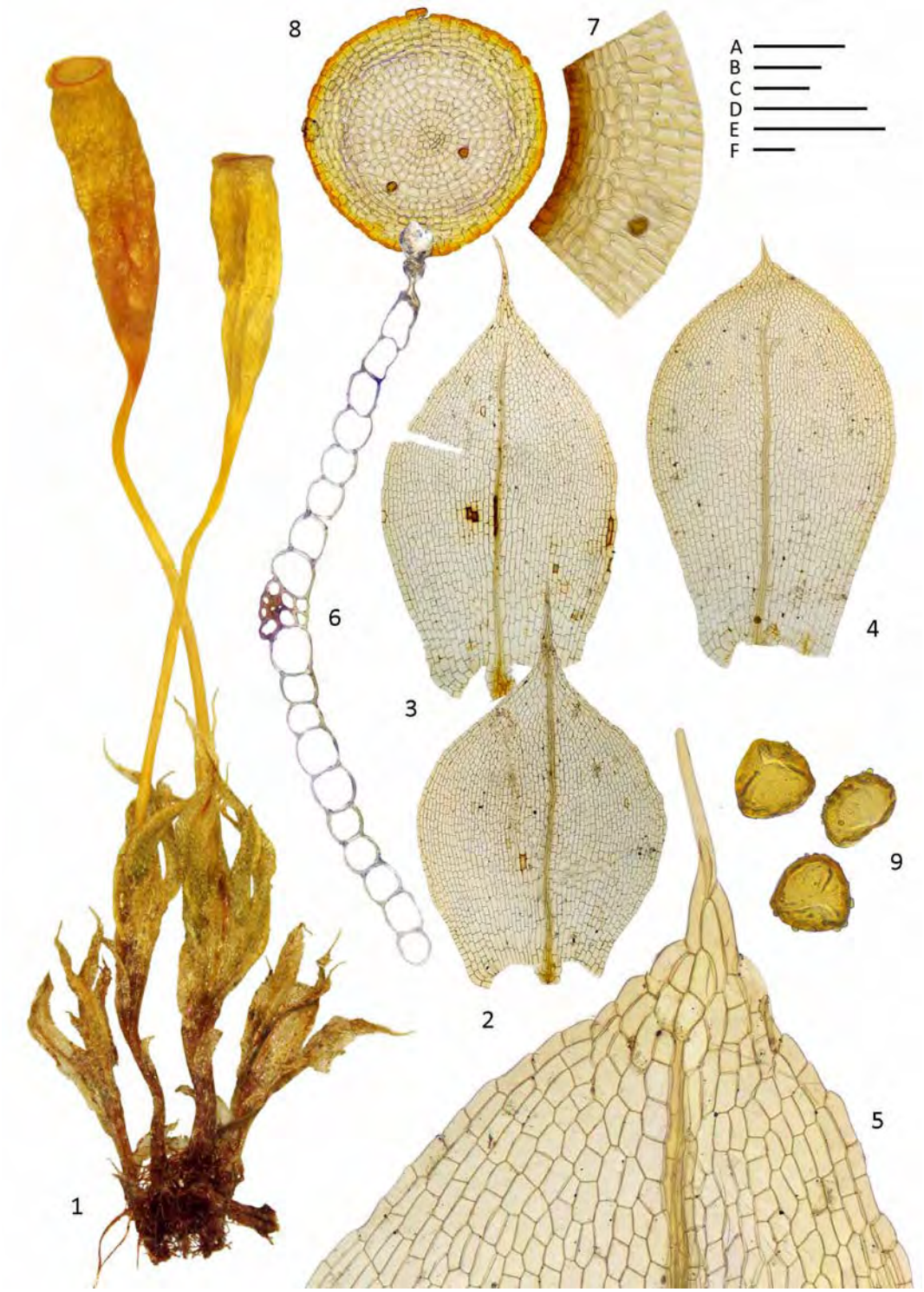

Figure 5.39: *Funariella clavata.* 1. Habit, dry (*N. Wilding 256*, BOL); 2–4. Leaves (2, 3 – *T.A.J. Hedderson 16854*, BOL; 4 – *T.A.J. Hedderson 16864*, BOL); 5. Leaf apex (*Bester 7079*, PRE); 6. Leaf cross-section (*N. Wilding 211*, BOL); 7. Capsule mouth & exothecial cells (as for 4); 8. Operculum (as for 2 & 3); 9. Spores (*N. Wilding 250*, BOL). Scale bars: A (2–4) = 500 µm; B (5, 7) = 100 µm; C (1) = 1 mm; D (6) = 100 µm; E (8) = 50 µm; F (6) = 100 µm.

Funariella mayottensis (Besch.) N. Wilding comb. nov. Basionym: *Streptopogon mayottensis* Besch., Ann. Sci. Nat. Bot., sér. 7, 2: 88 (1885); *Funaria mayottensis* (Besch.) Broth., Nat. Pflanzenfam. [Engler & Prantl] I(3): 419 (1904). –TYPE: COMOROS. Mayotte, Dzaoudzi, *M. Marie no. 14* (PC, lectotype!, designated here; isolectotypes in S!, NY!). The type of *S. mayottensis*, M. Marie No. 14 is present only at PC, S and NY. The only BM specimen is M. Marie 265 which is recorded as a type, however, it is not.

Illustration: Figure 5.41.

Plants medium to large, light–green. *Stems* reddish–brown, to 2.5 cm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. *Leaves* erect–spreading, contorted when dry, oblong–obovate to elliptical, 2–2.5 x 0.7–1.5 mm, plane to concave, strongly keeled, short–acuminate to apiculate, toothed in upper ½; *cells of upper lamina* quadrate or rhomboidal to oblong–hexagonal (32)43–58 x 17–38 µm; *basal* (57) 75–138 x (20)27–38 µm; *marginal cells* narrower, forming a border 1–2 cells wide in upper ⅓; *costae* percurrent to short excurrent.

Perigonia present. *Sporophytes* unknown.

Diagnostic Features

The combination of large, dentate, keeled leaves with percurrent to short excurrent costa is unique among the African species, making *Funariella mayottensis* easy to recognize.

Habitat and Distribution

The species is known only from the type locality on the island of Mayotte in the western Indian Ocean (Figure 5.40). No information on habitat is provided with the original material or in the description.

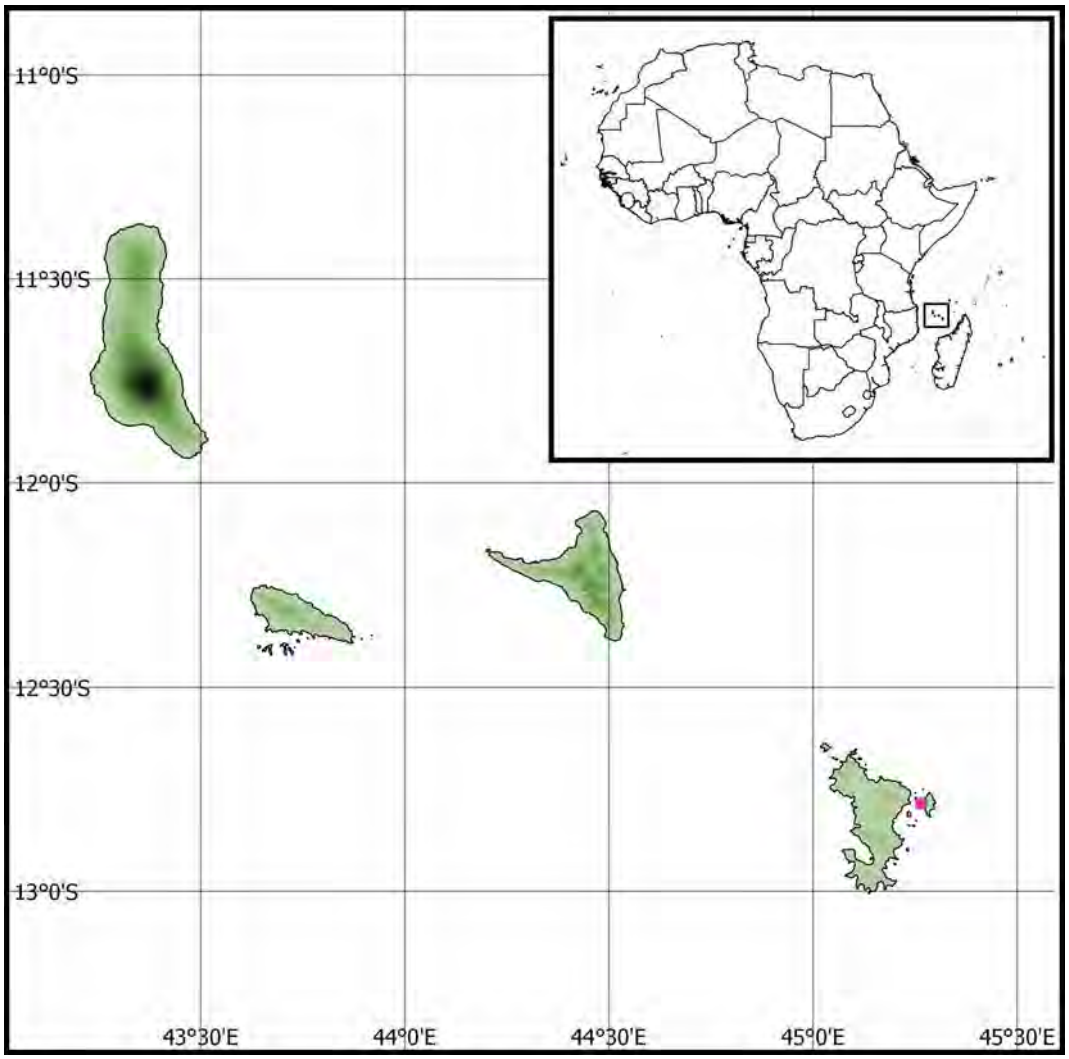

Figure 5.40: Distribution of *F. mayottensis* in Africa.

Note

The gametophytes of *F. mayottenis* are unusually long, judging by their length and the proportion of dead to green leaves, the gametophytes in the type collections have accumulate at least 2–3 years of growth, if not more. Examination of the type material revealed the production of multiple perigonial inflorences per plant, no perichaetia were observed.

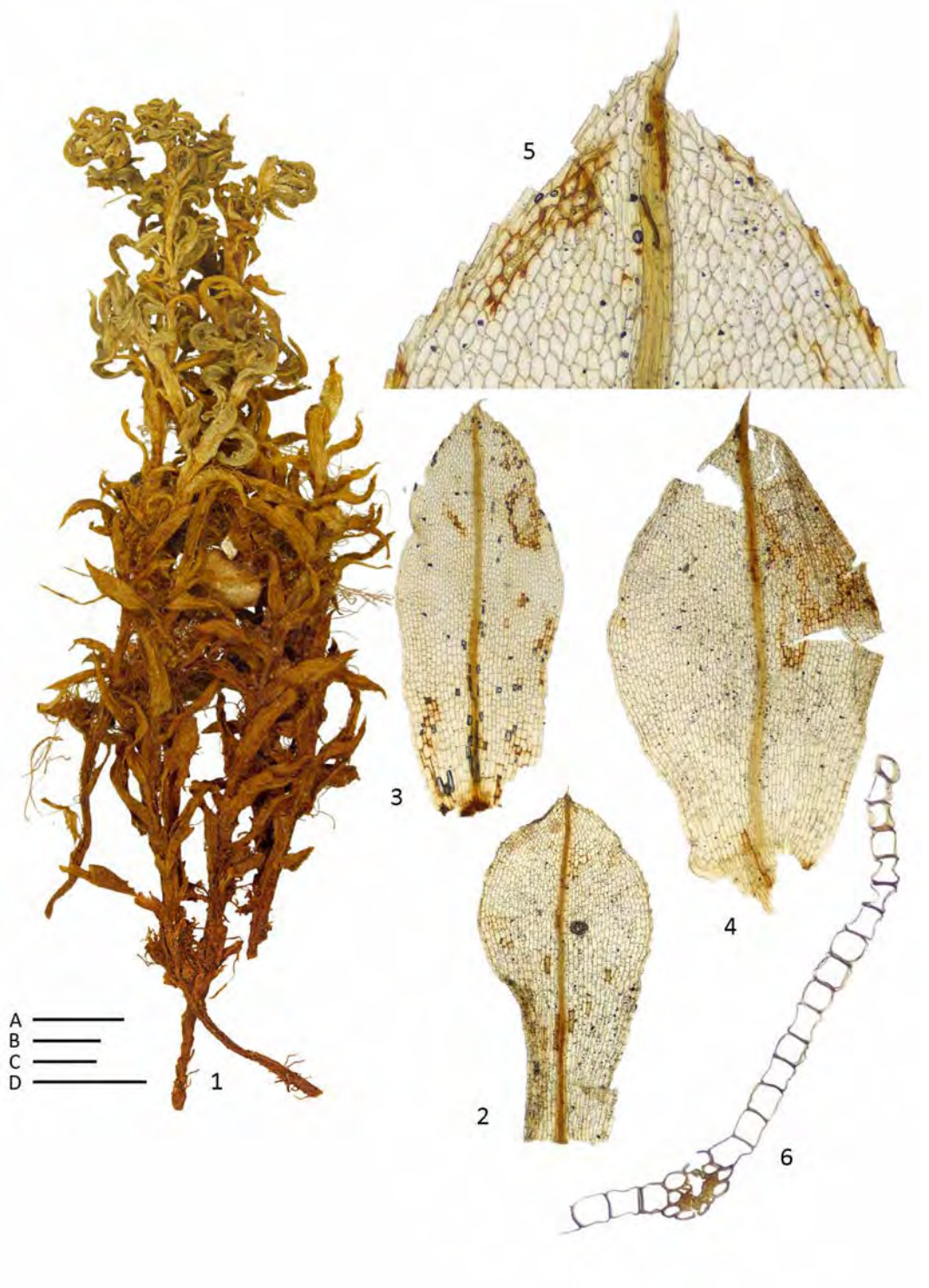

Figure 5.41: *Funariella mayottensis.* 1. Habit, dry; 2–4. Leaves; 5. Leaf apex; 6. Leaf cross-section. All from: *M. Marie no. 14*, PC. Scale bars: A (2–4) = 500 µm; B (5) = 100 µm; C (1) = 1 mm; D (6) = 100 µm.

Funariella sebapala N. Wilding sp. nov.–TYPE: LESOTHO. Top of Sani pass, mountain slopes, West of border post. Alpine heath–grassland, *ca.* 3000 m., *J. Van Rooy 3564* Feb. 1987 (PRE, holotype!; isotype in MO!).

The species is named after the Sebapala river, which is near to some of the first collections of the species.

Illustration: Figure 5.43.

Plants medium, light–green. *Stems* reddish–brown to 4 mm high, branching by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. *Leaves* erect–spreading, little contorted when dry, ligulate to obovate, 2.25–3 x 0.75–1.0 mm, slightly concave, short–acuminate, entire, aristate, arista to 600 µm; *cells of upper lamina* quadrate or rhomboidal to oblong–hexagonal, 30–63(75) x 20–40 µm; *basal* (33) 63–125 x 33–75; *marginal cells* undifferentiated; *costae* extending into apex and appearing excurrent in larger leaves.

Polyoicous. *Setae* 3–8 mm long, straight or slightly curved, yellow-orange, twisted anti-clockwise. *Capsules* erect or weakly inclined, slightly zygomorphic, oblong-obovoid, 1–2 x 0.4–0.8 mm, weakly constricted below mouth when dry, yellow to reddish–brown at maturity, with a well differentiated neck *ca*. ½ total length of capsule; *mouth* slightly oblique, *ca*. ¾ diameter of capsule; *exothecial cells* 40–83 x 13–25 µm, in cross-section with thick, strongly cuneate anticlinal walls, 4–6 rows of oblate cells at mouth. *Opercula* plano–convex, cells not twisted. *Peristome* double; *exostome teeth* straight, regular in shape, orange, tapered to an acute apex, to 210 µm high (often shorter and irregular in shape) and 88 µm wide at base, smooth to lightly papillose, striate; *endostome teeth* rudimentary, hyaline, to 50 µm high and 88 µm wide. *Spores* 27–30 µm, tetrahedral,

bacullate–insulate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

The ligulate to obovate, acuminate leaves, ± upright, peristomate capsules and bacullate–insulate spores set *F. sebapala* apart from other African species. *Funariella sebapala* can be confused with *F. succuleata* and *F. urceolata*. The former differs by having finely papillose spores with visible trilete scars while the latter differs by having longer, usually eperistomate capsules and lingulate to obovate acuminate leaves.

Habitat and Distribution

Funariella sebapala is known from the Drakensberg Mountains of South Africa and Lesotho (Figure 5.42). The species occurs in alpine heath grassland at elevations between 2100 m and 3000 m.

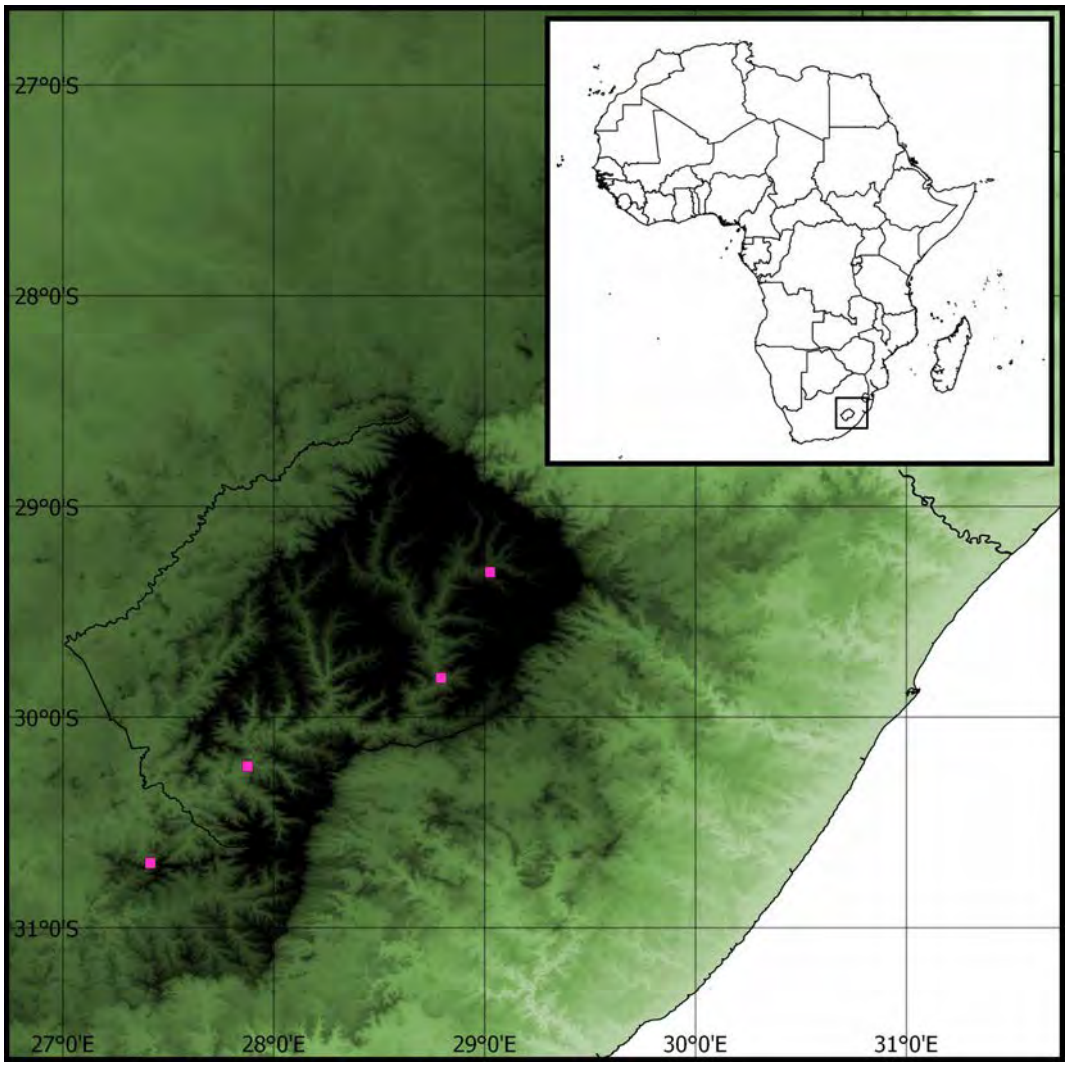

Figure 5.42: Distribution of *F. sebapala* in Africa.

Specimens Examined

LESOTHO. Mohlakwana, *R.E. Magill 4643*, 10/12/1977 (PRE, MO); Mokhotlong, *J. Van Rooy 3229, 3048*, x/2/1987 (MO); Taung, *R.E. Magill 4212*, 1/12/1977, *4213*, 1/12/1977, *4549*, 7/12/1977 (MO), *3209*, 1/2/1987 (PRE); Hlotse Valley, *J.G. Duckett & H.W. Matcham 1013a*, 21/4/1994 (BOL, MQU).

SOUTH AFRICA. Eastern Cape, Lady Grey, *J. Van Rooy 2723*, 1/2/1986 (PRE,

MO).

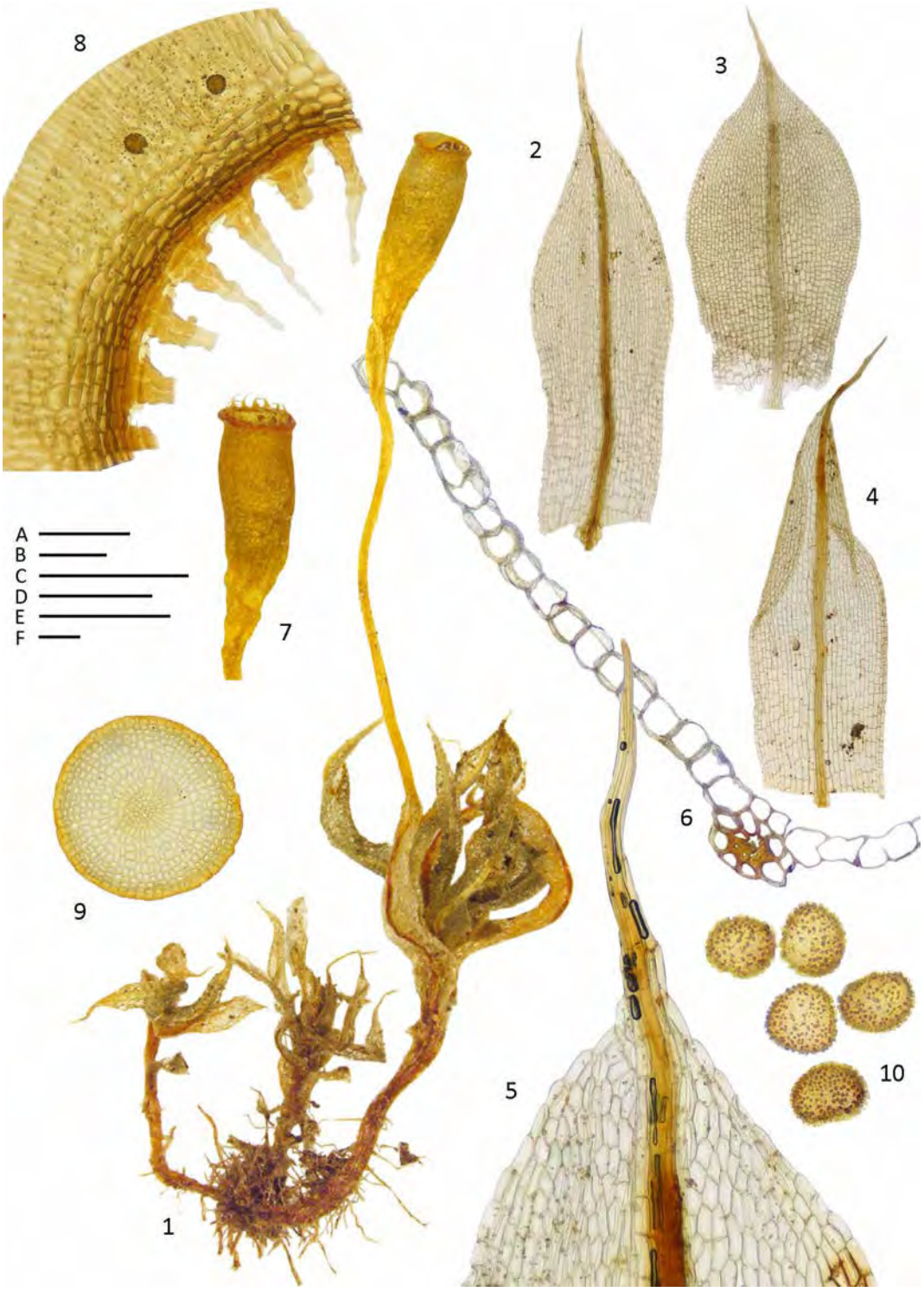

Figure 5.43: *Funariella sebapala.* 1. Habit, dry (*J. Van Rooy 3564*, PRE); 2–4. Leaves (*J. Van Rooy 3048*, PRE); 5. Leaf apex (as for 2–4); 6. Leaf cross-section (*J. Van Rooy 2723*); 7. Capsule, dry (as for 2–4); 8. Capsule mouth & exothecial cells (as for 2–4); 9. Operculum (as for 2–4); 10. Spores (as for 2–4). Scale bars: A (2–4) = 500 µm; B (5, 8) = 100 µm; C (1, 7) = 1 mm; D (6) = 100 µm; E (10) = 50 µm; F (9) = 100 µm.

Funariella spathulata (Schimp. ex Müll. Hal.) N. Wilding, Chapter 2. *Funaria spathulata* Schimp. ex Müll. Hal., Hedwigia 38: 61 (1899). *Entosthodon spathulatus* (Schimp. ex Müll. Hal.) Sim, Bryo. S. Afr. 298 (1926).–TYPE: SOUTH AFRICA. Western Cape, Groenekloof, *Breutel s.n.* (BM, holotype!; isotypes in S!, G!).

Illustration: Figure 5.45.

Plants medium, light–green. *Stems* reddish–brown, to 10 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. *Leaves* erect–spreading, contorted when dry, ovate to spathulate, 1.6–3.5 x 0.8–1.5 mm, plane to concave, short–acuminate to apiculate, often bluntly to sharply toothed by projecting cells in upper ½; *cells of upper lamina* quadrate or rhomboidal to oblong hexagonal, 33–60 x 18–30 µm; *basal* (25) 50–188 x (25) 38–63 µm; *marginal cells* undifferentiated; *costae* ending below apex.

Polyoicous. *Setae* 4–15 mm long, straight or slightly curved, pale-yellow to reddish–brown, twisted clockwise, bottom–half of seta sometimes twisted in opposite direction. *Capsules* inclined to horizontal, gibbous, zygomorphic, oblong-pyriform, 1–2.5 x 0.5–1.2 mm, weakly constricted below mouth when dry, yellow to reddish-brown at maturity, with a well differentiated neck *ca*. ½ total length of capsule; *mouth* oblique to almost transverse in some populations, *ca*. ¾ diameter of capsule; *exothecial cells* (20)25–63(70) x 10–18(25) µm, in cross-section with thick, strongly cuneate anticlinal walls, 4–6 rows of oblate cells at mouth. *Opercula* plano–convex to short conic, cells often twisted anti–clockwise from above. *Peristome* double; *exostome teeth* straight to sigmoidal, regular in

shape, orange to reddish, tapered to an acute apex, to 300 µm high and 75 µm wide at base, weakly papillose, striate, trabeculate, weakly appendiculate; *endostome teeth* smooth to finely papillose, hyaline, to 180 µm high and 100 µm wide. *Spores* 25–30 µm, tetrahedral, papillose to baculate–insulate or reticulate. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Funariella spathulata is the only species possessing a seta that is twisted clockwise from mid–way up.

Habitat and Distribution

Funariella spathulata is endemic to the Karoo regions of South Africa (Figure 5.44) occurring at elevations between 400 m and 1300 m. The species is infrequently encountered throughout its range.

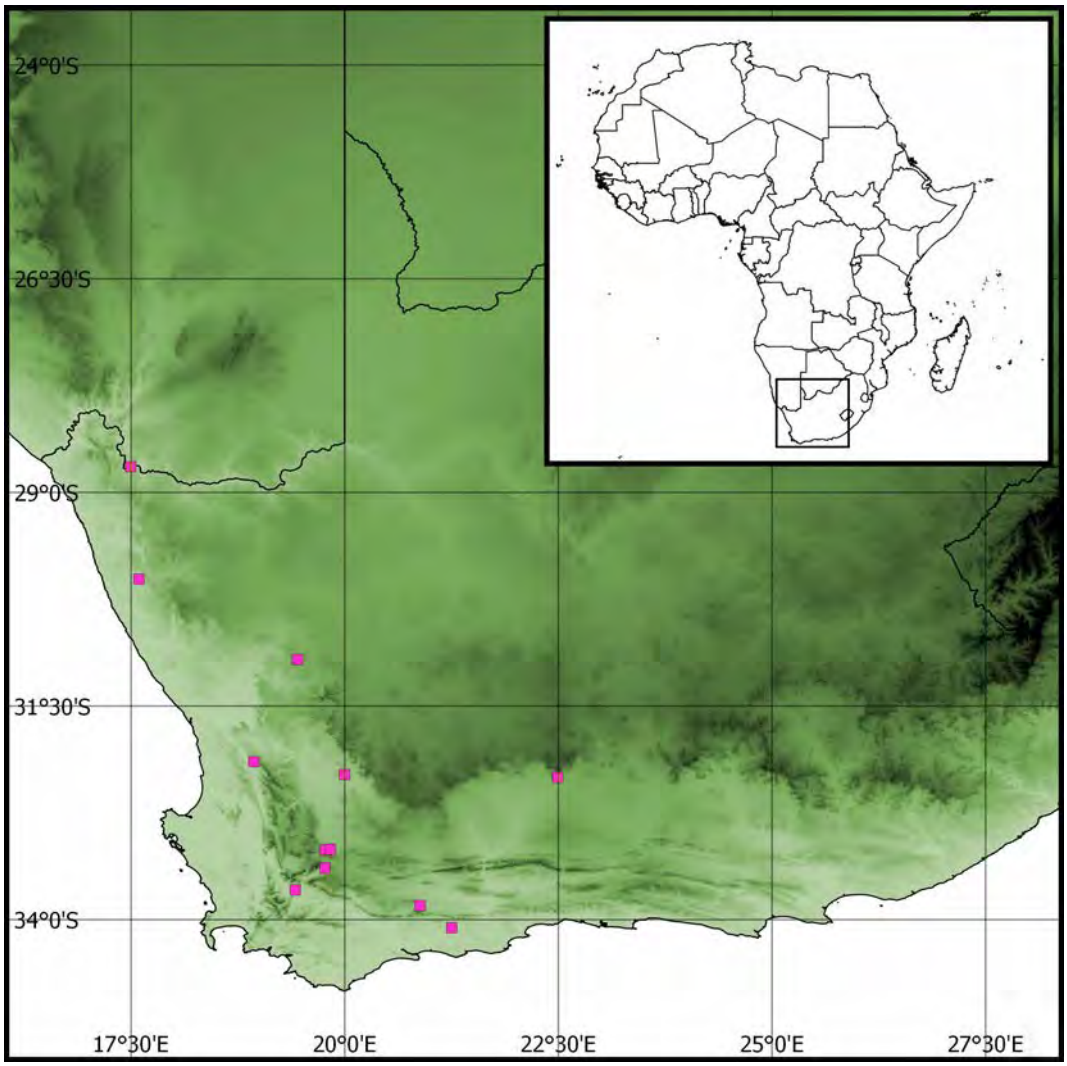

Figure 5.44: Distribution of *F. spathulata* in Africa.

Specimens Examined

SOUTH AFRICA.Northern Cape: Loeriesfontein, *N. Wilding 251*, 18/9/2010 (BOL); Nieuwoudtville, *N. Wilding 255*, 1/8/2011 (BOL); Richtersveld, Stinkfontein Mt., *Oliver, Toelken & Venter 647*, 4/9/1977 (E, MO); Tankwa Karoo N.P., *S.P. Bester 7124*, 6/8/2006 (PRE, MO); Petrusville, *H. Vahrmeijer CH12648*, x/12/1977 (MO); Namaqua N.P., *S.P. Bester 5910*, 16/8/2005

(PRE); Western Cape: Beaufort West, *T.A.J. Hedderson 16914*, 31/2/2009 (BOL); Barrydale, *T.A.J. Hedderson 16478*, 3/9/2007 (BOL); Clanwilliam, *N. Wilding 212a, 212b, 213a, 213b*, 7/9/2011 (BOL); Ceres District, *T.A.J. Hedderson 13859, 13860*, 4/6/2001, *17054* (BOL); Worcester, *E. Esterhuysen 31978,* 17/8/1968 (BOL); Hex River Pass, *E.A. Schelpe 4917*, 9/10/1954 (BOL, PRE); Riversdale, *J. Muir 3717*, 19/9/1925 (MO); Karoo N.P., *S.P. Bester 6191*, 8/12/2005 (PRE, MO).

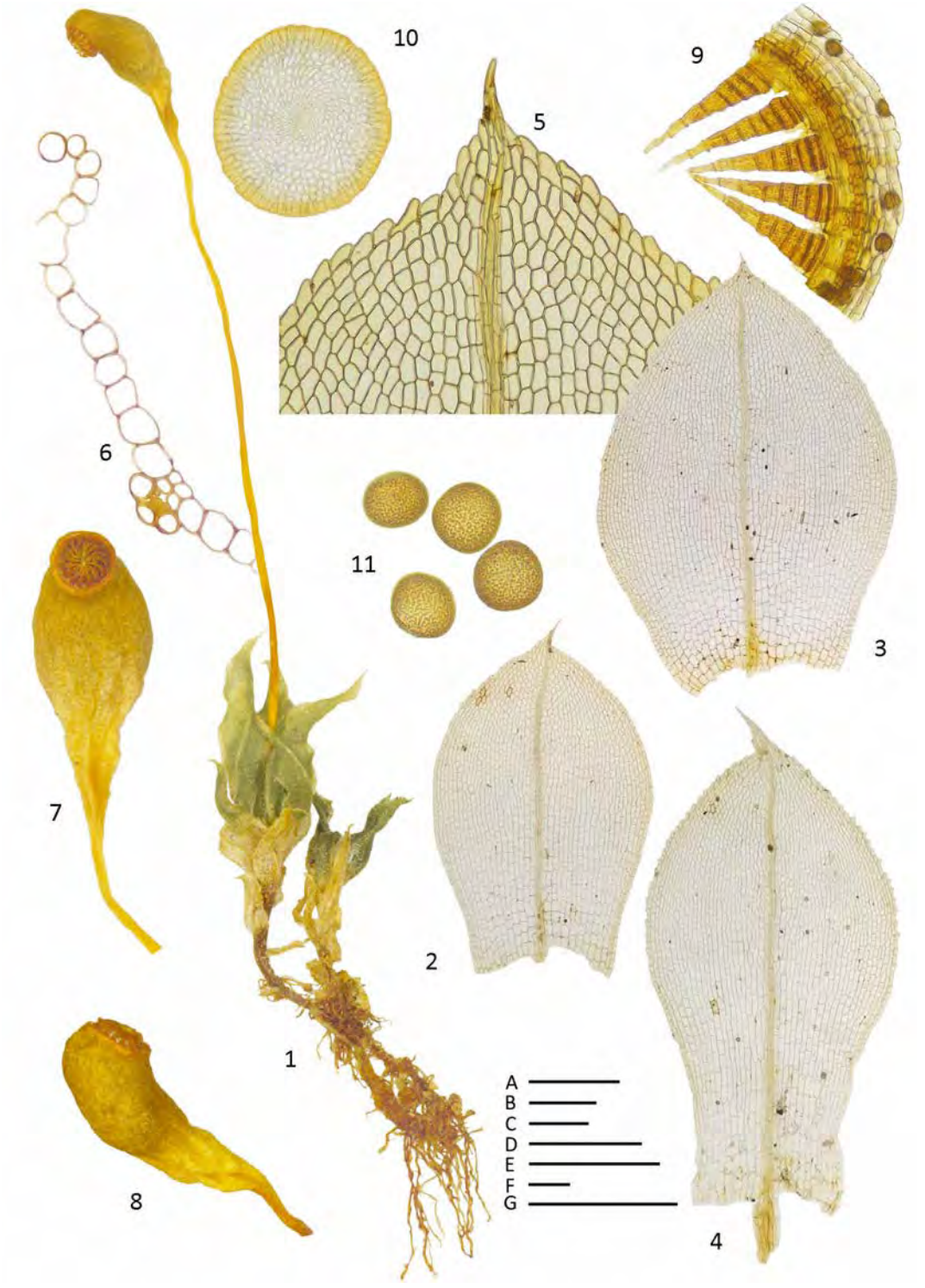

Figure 5.45: *Funariella spathulata.* 1. Habit, dry (*N. Wilding 212a*, BOL); 2–4. Leaves (2, 3 – *N. Wilding 255*, BOL; 4 – as for 1); 5. Leaf apex (as for 2 & 3); 6. Leaf cross-section (*T.A.J. Hedderson 16478*, BOL); 7, 8. Capsule, dry (as for 6); 9. Capsule mouth & peristome (*T.A.J. Hedderson 17054*, BOL); 10. Operculum (as for 1); 11. Spores (as for 6). Scale bars: A (2–4) = 500 µm; B (5, 9) = 100 µm; C (1) = 1 mm; D (6) = 100 µm; E (11) = 50 µm; F (10) = 100 µm; G (7, 8) = 1 mm.

Funariella succuleata (Wager & Wright) N. Wilding, Chapter 2. *Physcomitrium succuleatum* Wager & Wright, Trans. R. Soc. S. Afr. 4:3 (1914). *Funaria succuleata* (Wager & Wright) Magill, Fl. S. Africa Bryophyta 2: 321 (1987).–TYPE: SOUTH AFRICA. KwaZulu–Natal, Rydal Mount, *Wager s.n.* (PRE, holotype! (PRE–CH12075); isotypes in BM!).

Synonyms:

Funaria dieterlenii Thér., Bull. Mus. Hist. Nat. (Paris) 30: 240 (1924).–TYPE: LESOTHO. Leribe, *Dieterlen s.n.* (PC, holotype!).

Illustration: Figure 5.47.

Plants small, light–green. *Stems* orangish–brown, to 10 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. *Leaves* erect–spreading, little contorted when dry, ovate to obovate or spathulate, (1.4)1.7–2.5(2.8) x (0.6)0.8–1.25 mm, plane or concave, short acuminate to apiculate, entire to weakly toothed in upper ⅓; *cells of upper lamina* quadrate to oblong–hexagonal, 16–32(40) x 8–16 µm; *basal* 48–155 x 25–45 µm; *marginal cells* undifferentiated; *costae* ending below the apex, rarely percurrent.

Polyoicous. *Setae* 3–5 mm long, straight, pale–yellow to reddish–brown, twisted anti–clockwise. *Capsules* erect to inclined, gibbous, zygomorphic, oblong-pyriform, not or weakly constricted below mouth when dry, 1.4–2.1 x 0.5–0.7 mm, yellow to reddish–brown at maturity, with a well differentiated neck *ca*. ½ total length of capsule; *mouth* slightly oblique, *ca*. ¾ diameter of capsule; *exothecial cells*, (38)50–63 x 10–23 µm, in cross-section with thick, strongly cuneate anticlinal walls, 3–6 rows of oblate cells at mouth; *opercula* plano–convex, cells not or

slightly twisted from above. *Peristome* double; *exostome teeth* straight, regular in shape, orange, tapered to an acute apex, to 258 µm high, *ca.* 22 µm wide at base, becoming hyaline in upper ⅓, papillose, striate, trabeculate, weakly appendiculate; *endostome teeth* rudimentary, irregular in shape, pale-yellow to hyaline, finely papillose, to *ca.* 20 µm high and 25 µm wide. *Spores* (25)27–35(38) µm, tetrahedral, collapsed, finely papillose, trilete scars visible. *Calyptrae* cucullate, rostrate.

Diagnostic Features

The combination of entire leaves, zygomorphic, peristomate capsules and spores with visible trilete scars clearly distinguishes *F. succuleata*. Macroscopically, the species can be confused with *F. spathulata*, however, the almost smooth spores of *F. succuleata* clearly set it apart.

Habitat and Distribution

Funariella succuleata is largely restricted to the Drakensberg and surrounding high mountains of Lesotho and South Africa (Figure 5.46). The species occurs in shrubland and grassland at elevations between 1300 m and 2100 m.

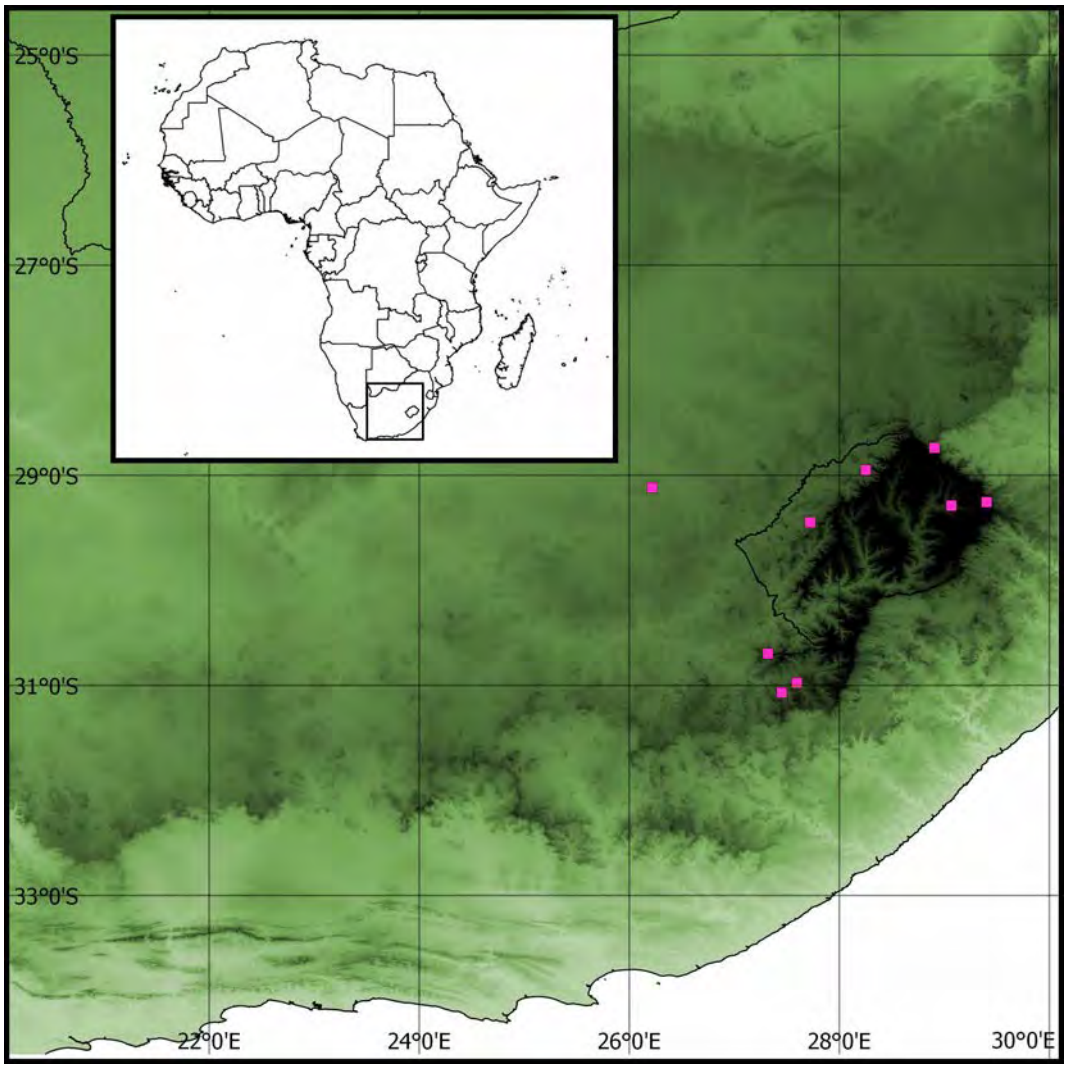

Figure 5.46: Distribution of *F. succuleata* in Africa.

Note

The leaves from Lesotho collections often have a distinctive glaucous look about them.

Specimens Examined

LESOTHO. Mokhotlong, *J. Van Rooy 3180, 3183, 3260*, x/2/1987 (MO), *3289,*

3343, 3369, x/2/1986 (PRE), *4658*, 10/12/1977 (PRE, MO); Leribe, *A. Dieterlen 686B* (MO), *686* (PRE); Taung, *R.E. Magill 4221, 4226*, 1/12/1977 (PRE, MO); 16 km West of Oxbow Lodge, *R.E. Magill 4622*, 8/12/1977 (E, MO); Roma, *M. Schmitz 8111*, 1/8/1977 (PRE);

SOUTH AFRICA. Eastern Cape: Lady Grey, *J. Van Rooy 2633, 2690, 2703*, 1/2/1986 (PRE, MO); Barkly East, *J. Van Rooy 2760*, 1/2/1986 (PRE), *Welsh s.n*. 16/7/1964 (MO); Free State: Bloemfontein, *Prof. Potts s.n.,* 5/3/1917 (PRE CH9535); KwaZulu–Natal: Cannibal Caves, *Miss Edwards s.n*., 1/8/1922 (PRE); Rydal Mount, *H.A. Wager 281*, 1/12/1910 (PRE).

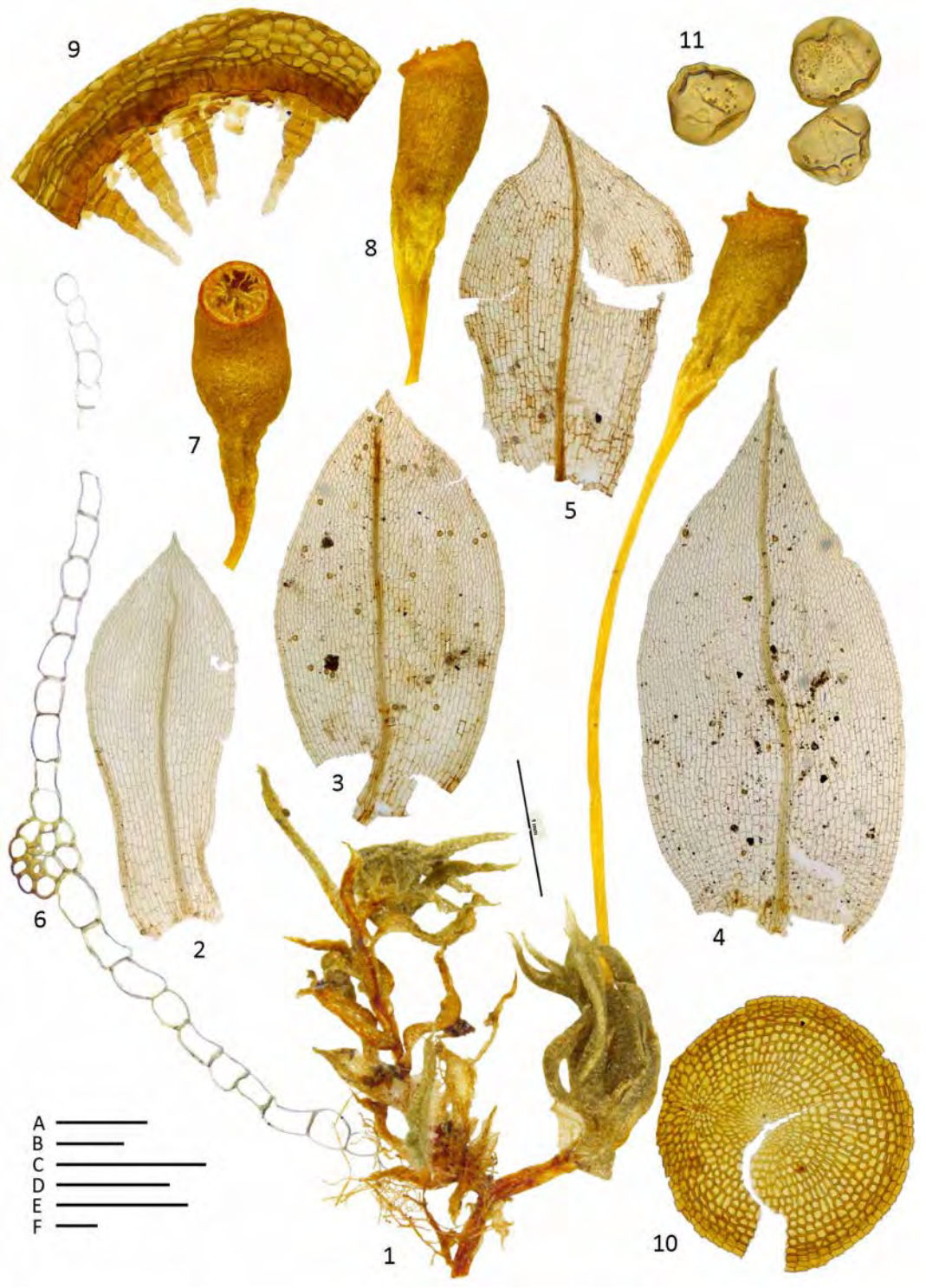

Figure 5.47: *Funariella succuleata.* 1. Habit, dry (*J. Van Rooy 2703*, PRE); 2–5. Leaves (2 – *R.E. Magill 4658*, PRE; 3, 5 – *M. Schmitz 8111*, PRE; 4 – *J. Van Rooy 3289*, PRE); 6. Leaf cross-section (as for 4); 7, 8. Capsule, dry (as for 1); 9. Capsule mouth & peristome (as for 4); 10. Operculum (as for 3 & 5); 11. Spores (*Welsh s.n.*, MO). Scale bars: A (2–5) = 500 µm; B (9) = 100 µm; C (1, 7, 8) = 1 mm; D (6) = 100 µm; E (11) = 50 µm; F (10) = 100 µm.

Funariella sulcata N. Wilding sp. nov.–TYPE: NAMIBIA. Windhoek, road through Khomas and Hochland, 8/7/1979, *H.M. Anderson 6* (PRE, holotype!). The species name is derived from the sulcate appearance of the capsule neck, when dry. Although not unique within the family, this feature stood-out upon first examination of the species.

Illustration: Figure 5.49.

Plants medium, light–green. *Stems* orangish–brown, to 10 mm high, branching once or multiple times by sub–perigonial innovation, in cross-section with one layer of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. *Leaves* erect–spreading, little contorted when dry, oblong–obovate to spathulate, 2.2–2.8 x (0.5)0.9–1.25 mm, slightly concave, short acuminate, entire to weakly serrate in upper ⅓, aristate, arista to 55 µm; *cells of upper lamina* roughly rectangular to oblong–hexagonal, (35)42–75(88) x 17–33 µm, *basal* (37)57–138(160) x (25)32–45(55) µm, *marginal cells* undifferentiated; *costae* ending below apex.

Polyoicous. *Setae* 3–6 mm long, straight, pale–yellow to reddish–brown, twisted anti-clockwise. *Capsules* inclined to horizontal, gibbous, zygomorphic, oblong-pyriform, 1.4–1.8 x 0.5–0.7 mm, weakly constricted below mouth when dry, light–brown at maturity, with a well differentiated neck *ca*. ½ total length of capsule; *mouth* slightly oblique, *ca*. ¾ diameter of capsule; *exothecial cells*, 30–55(73) x 10–18(25) µm, in cross-section with thick, strongly cuneate anticlinal walls, 3–7 rows of oblate cells at mouth. *Opercula* short–conic, cells twisted anti–clockwise from above. *Peristome* double; *exostome teeth* straight, regular in shape, orange, tapered to an acute apex, to 330 µm high, *ca*. 58 µm wide at base, smooth, striate, trabeculate; *endostome teeth* straight, pale-yellow, striate, finely papillose, to 263

µm high and 58 µm wide. *Spores* 12–23 µm, tetrahedral, smooth to finely papillose, often collapsing, trilete scars inconspicous. *Calyptrae* cucullate, rostrate.

Diagnostic Features

The aristate leaves, short conic operculum and small, smooth to finely papillose spores set it apart from other African species.

Habitat and Distribution

Funariella sulcata is known from only four populations in Namibia (Figure 5.48) where it occurs in Savannah/grassland at elevations of *ca*. 1150 m.

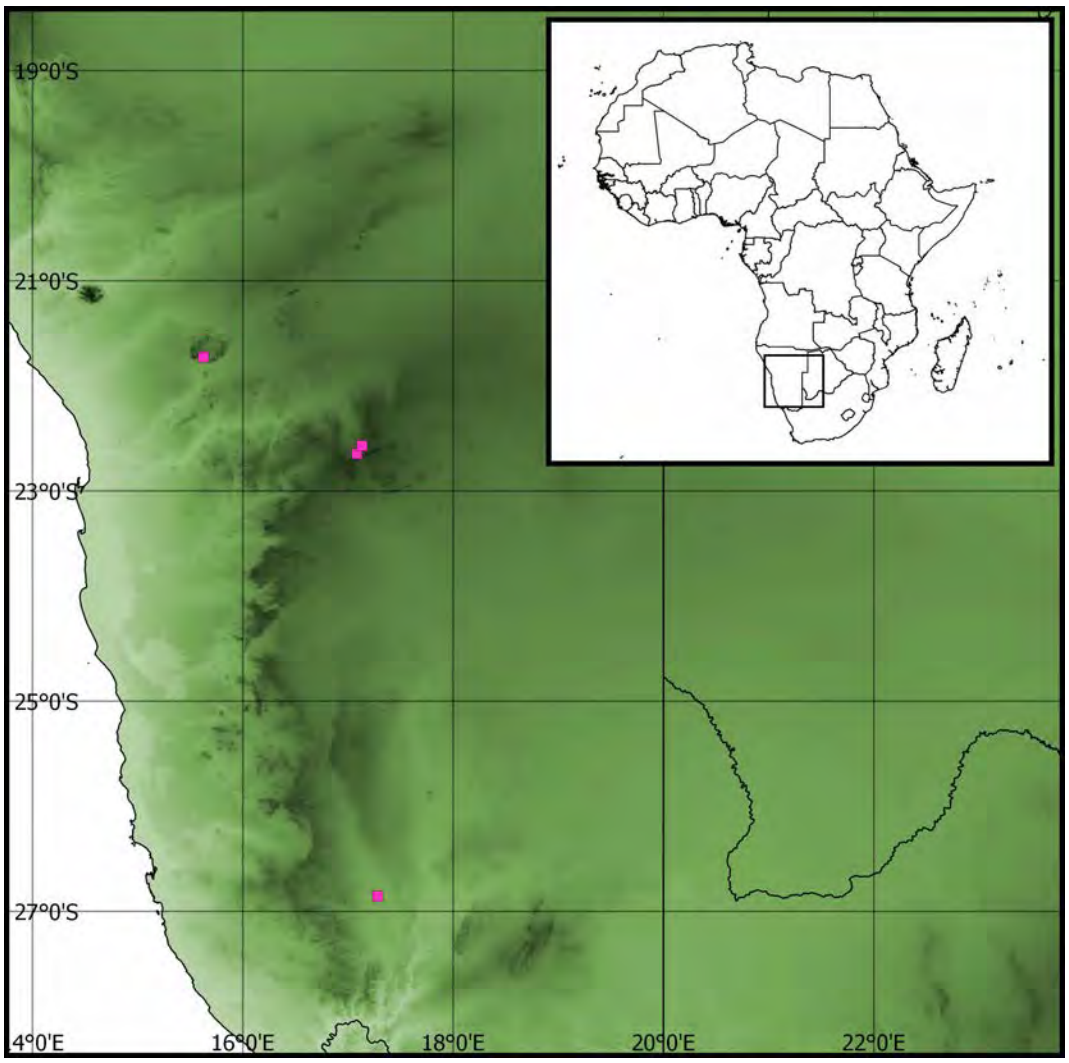

Figure 5.48: Distribution of *F. sulcata* in Africa.

Specimens Examined

NAMIBIA. Erongo Mnts., *H.M. Anderson 14a,* 11/7/1979 (PRE, MO); Khomas (Windhoek district), *C.A. Mannheimer 196A*, 10/3/1996 (PRE); Karas (Rooiberg) ridge, *C.A. Mannheimer & J. Mannheimer 413*, 29/9/1996 (PRE).

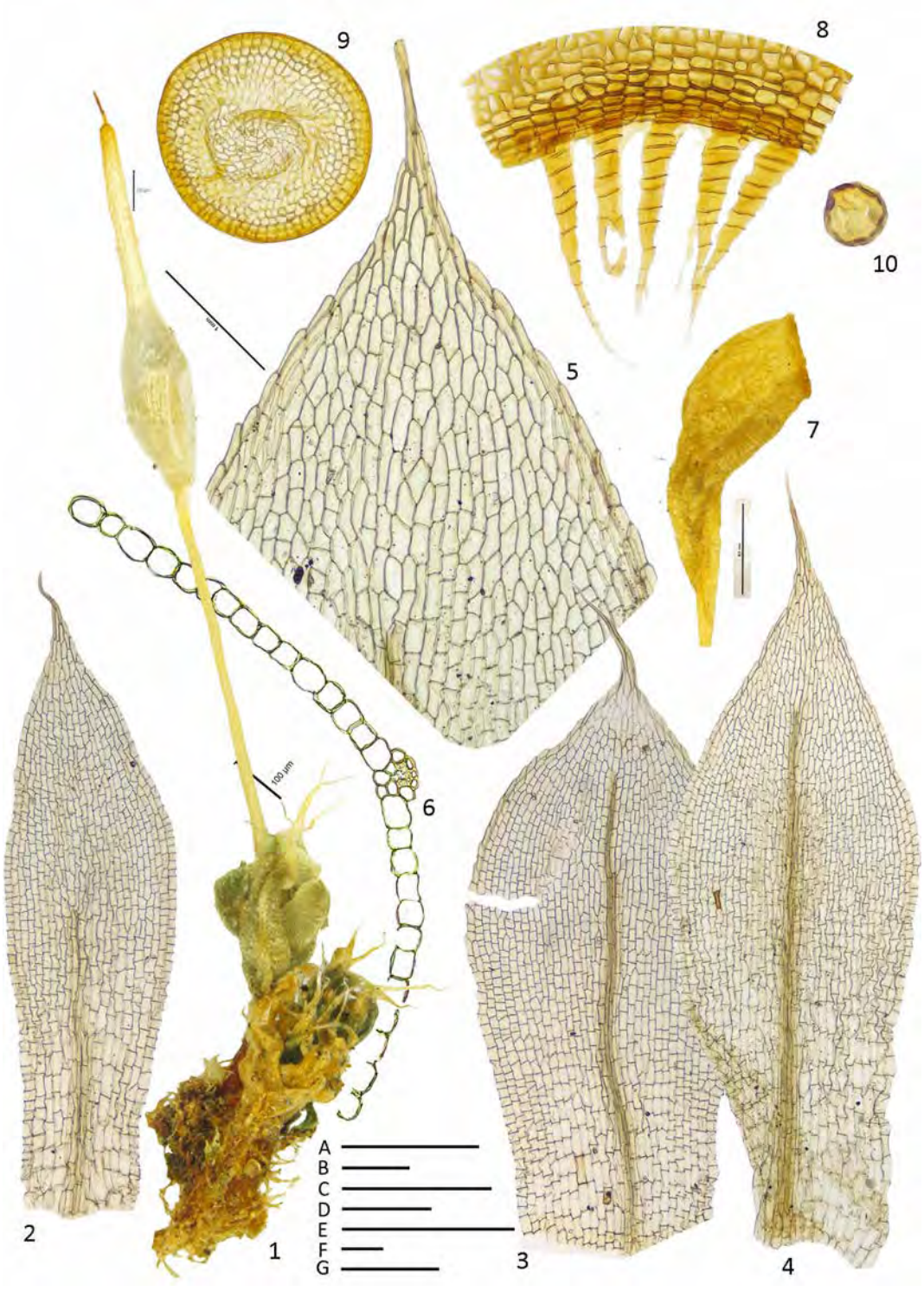

Figure 5.49: *Funariella sulcata.* 1. Habit, dry (*C.A. Mannheimer & J. Mannheimer 413*, PRE); 2–4. Leaves (*H.M. Anderson 6*, PRE); 5. Leaf apex (as for 2–4); 6. Leaf cross-section (as for 1); 7. Capsule, dry (as for 2–4); 8. Capsule mouth & peristome (as for 1); 9. Operculum (as for 1); 10. Spores (as for 2–4). Scale bars: A (2–4) = 500 µm; B (5, 8) = 100 µm; C (1) = 1 mm; D (6) = 100 µm; E (10) = 50 µm; F (9) = 100 µm; G (7) = 500 µm.

Funariella urceolata (Mitt.) N. Wilding, Chapter 2. *Entosthodon urceolatus* Mitt., Thes. Cap. 1:63 (1859). *Funaria urceolata* (Mitt.) Magill, Mem. Bot. Surv. South Africa 43:7 (1979).–TYPE: SOUTH AFRICA. Eastern Cape, East London, *Rooper s.n.* (NY, holotype!).

Synonyms:

Funaria rufinervis Dixon, Trans. Roy. Soc. South Africa 18:254 (1930).–TYPE: SOUTH AFRICA. KwaZulu–Natal, National Park, *Wager 758* (BM, holotype!; isotypes in PRE!, MO!).

Illustration: Figure 5.51.

Plants medium to large, dark green. *Stems* reddish–brown, to 4 mm high, branching multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. *Leaves* erect–spreading, lingulate to oblong–obovate, (2)2.2–5.2 x (0.3)0.5–1.3(1.5) mm, plane to slightly concave, short acuminate, entire, aristate, arista to 300 µm; *cells of upper lamina* rhomboidal to hexagonal or oblong–hexagonal, (32)37–70(88) x (12)20–30(38) µm; *basal* 67–175(225) x (17)27–40(46) µm; *marginal cells* sometimes bulging distally near apex; costae excurrent, less frequently ending below the apex.

Polyoicous. *Setae* 4–9 mm long, straight, pale–yellow to reddish–brown, twisted anti–clockwise. *Capsules* inclined to horizontal, zygomorphic, oblong–obovoid, 2–2.8 x 0.7–0.9 mm, constricted below mouth when dry, reddish–brown at maturity, with a well differentiated neck *ca*. ½ the total length of the capsule; *mouth* transverse *ca*. ⅔ the diameter of the capsule; *exothecial cells* (40)50–88(98) x (10)15–25 µm, in cross-section with thick, strongly cuneate anticlinal walls, 3–5

rows of oblate cells at mouth. *Opercula* plano–convex, cells not twisted. *Peristome* usually absent, if present single; *exostome teeth*, pale orange at base, mostly hyaline above, 150 µm long and 32 µm wide at base. *Spores* (22)30–38 µm, tetrahedral, low baculate to verrucate–lirate, trilete scars often visible on spores which have finely verrucate, lirate ornamentation. *Calyptrae* cucullate, rostrate.

Diagnostic Features

Funariella urceolata is recognized by its large lingulate to oblong–obovate leaves and its zygomorphic, oblong–pyriform capsules with bacullate to verrucate–lirate spores.

Habitat and Distribution

The species occurs in the southern and eastern parts of South Africa and the eastern parts of Zimbabawe (Figure 5.50). *Funariella urceolata* is known from elevations up to 1700 m.

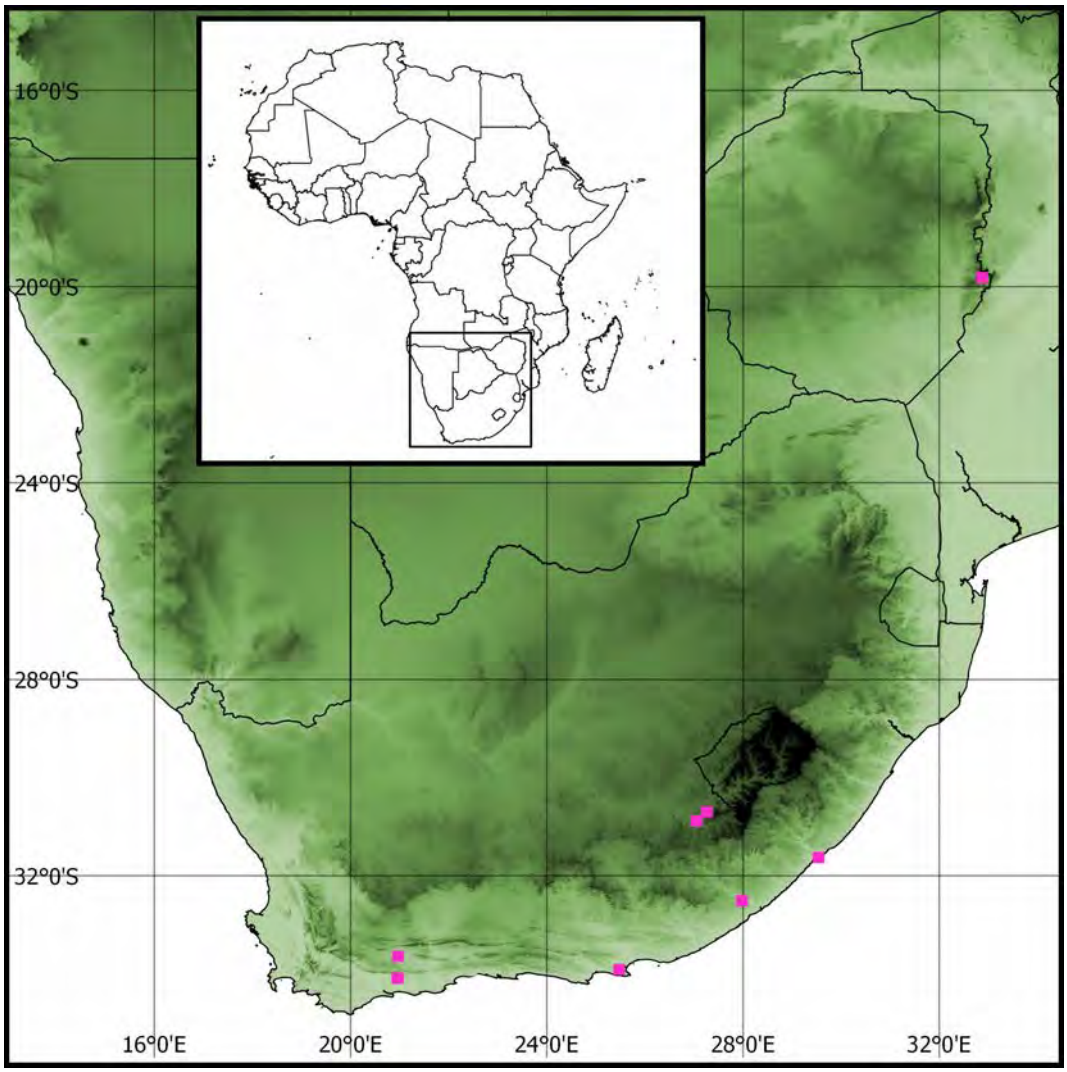

Figure 5.50: Distribution of *F. urceolata* in Africa.

Note

When the leaves of *F. urceolata* are not strongly lingulate and leaf shape begins to resemble *F. campylopodioides* the species can be difficult to distinguish. The two species have almost identical capsules and possibly the same range of spore ornamentation. The only obvious difference is in the size and the shape of the leaves. Can further be confused with *Fifeobryum longicollis* , see Notes under

this species.

Specimens Examined

SOUTH AFRICA. Eastern Cape: Port St. Johns, *Wager 11697* (MO); Rhodes, *M. Koekemoer 1496*, 7/12/1999 (MO); Lady Grey, *J. Van Rooy 2662*, x/2/1986 (MO); Port Elizabeth, T.R. *Sim 10126*, 1922 (PRE); Kei bridge, *R. Ellis 3103*, 13/7/1977 (PRE); KwaZulu–Natal: Goodoo Forest, *Wager 11672* (PRE, MO); Western Cape: Heidelberg, *N. Wilding 247*, 7/10/2010 (BOL); Touwsberg, *L. Smook 8748*, 10/7/1993 (MO).

ZIMBABWE. Adams 597, 579, 26/5/1988 (MO).

Figure 5.51: *Funariella urceolata.* 1. Habit, dry (*J. Van Rooy 2662*, MO); 2, 3. Leaves (as for 1); 4. Leaf apex (*N. Wilding 247*, BOL); 5. Leaf cross-section (*Wager 560*, PRE); 6. Capsule, dry (as for 4); 7. Capsule mouth & peristome (*Wager 11672*, PRE); 8. Operculum (as for 7); 9. Spores (*Rooper s.n.*, NY). Scale bars: A (2, 3) = 500 µm; B (4, 7) = 100 µm; C (1) = 1 mm; D (5) = 100 µm; E (9) = 50 µm; F (8) = 100 µm; G (6) = 1 mm.

5.4.6. *Physcomitrellopsis* Broth. & Wager

Physcomitrellopsis Broth. & Wager, J. Bot. 60: 107 (1922).–TYPE: *Physcomitrellopsis africana* Wager & Broth. ex Dixon, J. Bot. 60: 107 (1922).

Plants small, gregarious, green to dark green. Stems orange–brown, to 3 mm, branching once by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled, orangish cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. Leaves erect–spreading, contorted when dry, plane, oblong-obovate to spathulate, 2–4.8 x 1–1.8 mm, short-acuminate to apiculate, margins strongly toothed in upper ½ to ⅔ by obtuse projecting cells, entire below; cells of upper lamina thin-walled, rhomboidal to oblong hexagonal, 43–70 x 25–38 µm; basal cells rectangular, thinner-walled, longer and laxer, 11–188 x 25–55 µm; marginal cells undifferentiated; costae ending below the apex, rarely percurrent. Axillary-hairs present, hyaline, multicellular, uniseriate, the apical cell largest and with rounded end walls. Polyoicous. Perigonia single terminating primary shoot, synoicous shoot arising by sub–perigonial innovation. Paraphyses club–shaped. Setae 0.4–0.8 mm long, reddish–brown, not twisted, straight to curved. Capsules erect to weakly inclined, radially symmetric, globose, 0.8–1.2 x 0.6–0.8 mm, reddish–brown at maturity, sulcate when dry, with a neck *ca*. ¼ the total length of the capsule, cleistocarpic; exothecial cells, 23–52 x 20–35 µm, mostly isodiamteric or hexagonal, becoming more oblate near mouth, in cross-section with unthickened anticlinal walls. Opercula retained, planar, cells not twisted. Peristome absent. Spores, tetrahedral, 28–38 µm, collapsed, weakly papillose, trilete scars visible. Calyptrae mitrate, 4–5 lobed at base, rostrate, papillose.

The genus comprises the sole Southern African species.

Physcomitrellopsis africana Wager & Broth. ex Dixon., J. Bot. 60: 107 (1922).–TYPE: SOUTH AFRICA. Natal, *Wager s.n.* (H, holotype; isotype in BM!).

Illustration: Figure 5.53.

Plants medium, dark green. *Stems* orange–brown, to 3 mm high, branching once to multiple times by sub–perigonial innovation, in cross-section with 1–2 layers of thick-walled cortical cells, a hyalodermis and a central strand, rhizoids reddish–brown. *Leaves* erect–spreading, contorted when dry, oblong-obovate to spathulate, 2–4.8 x 1–1.8 mm, short-acuminate to apiculate, strongly toothed in upper ½ to ⅔ by obtuse projecting cells; *cells of upper lamina* rhomboidal to hexagonal or oblong hexagonal 43–70 x 25–38 µm; *basal* 11–188 x 25–55 µm; *marginal cells* undifferentiated; *costae* ending below the apex, rarely percurrent.

Polyoicous. *Setae* 0.4–0.8 mm long, straight or curved, reddish–brown. *Capsules* erect to weakly inclined, globose, radially symmetric, 0.8–1.2 x 0.6–0.8 mm, cleistocarpic, sulcate when dry, with a neck *ca*. ¼ the total length of the capsule, reddish–brown at maturity; *exothecial cells*, 23–52 x 20–35 µm, mostly isodiamteric, becoming more oblate near mouth, in cross-section with unthickened anticlinal walls. *Opercula* retained, planar, cells not twisted. *Peristome* absent. *Spores* 28–38 µm, tetrahedral, collapsed, weakly papillose, trilete scars visible. *Calyptrae* mitrate, rostrate, papillose.

Diagnostic Features

Physcomitrellopsis africana is unique in the family by virtue of its papillose calyptrae. The presence of a small, incipient, indehiscent operculum easily sets it apart from other genera with immersed, cleistocarpic capsules such as *Physcomitrella,*

Cygnicollum and *Bryobeckettia*. Additionally, the combination of immersed capsules and finelly papillose spores bearing trilete scars is not seen anywhere else in the family.

Habitat and Distribution

This species is known from the edge of coastal forests the in Eastern Cape and KwaZulu–Natal (Figure 5.52). The exact locality of the Type was not given and the site has not been located. *Physcomitrellopsis africana* can be found in habitats typical of members of *Entosthodon s.l.*, i.e. on moist shaded soil in sheltered crevices or at the base of low vegetation.

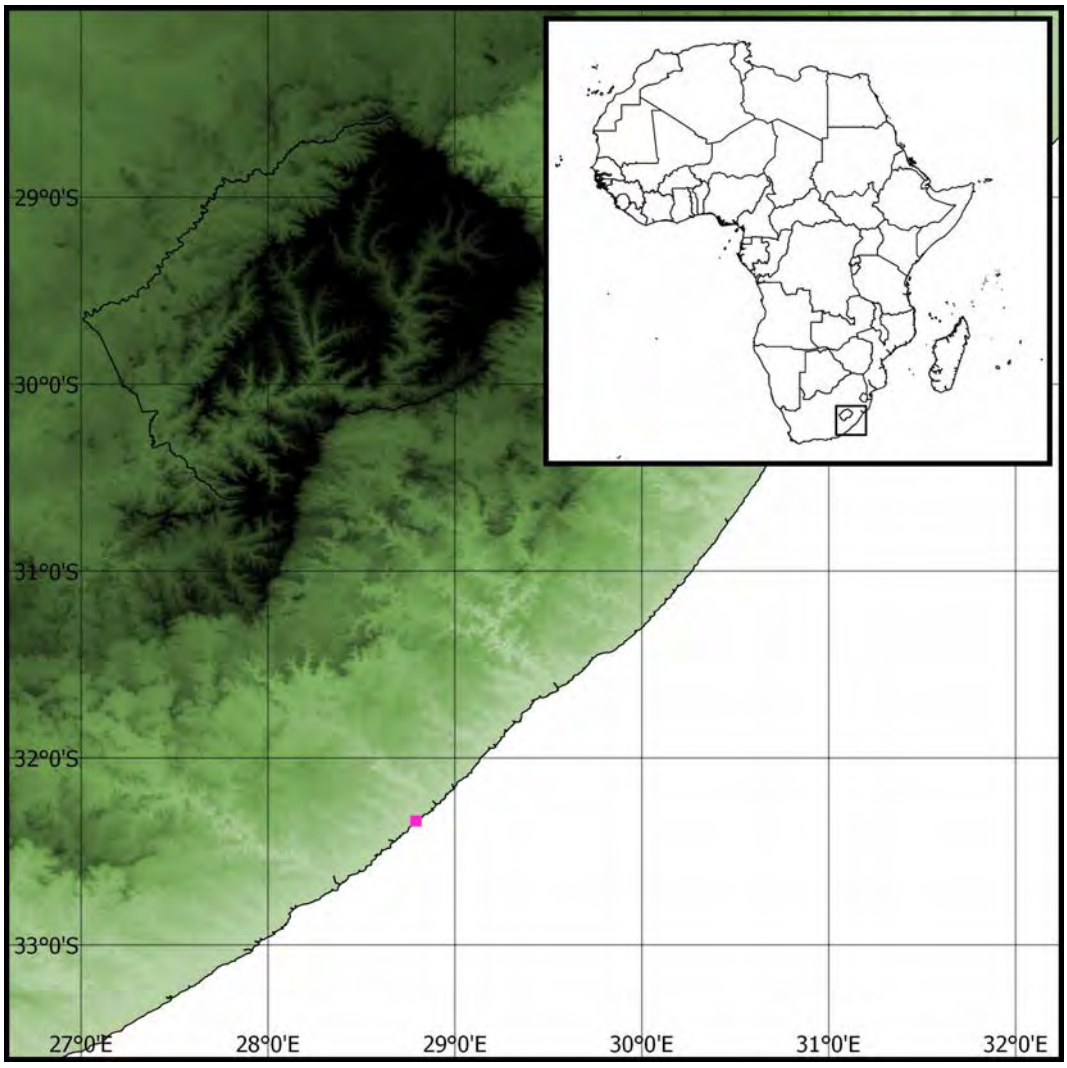

Figure 5.52: Distribution of *P. africana* in Africa.

Specimens Examined

SOUTH AFRICA. Eastern Cape, Dweza, *T.A.J. Hedderson 17571, 17577, 17580*, 10/10/2010 (BOL).

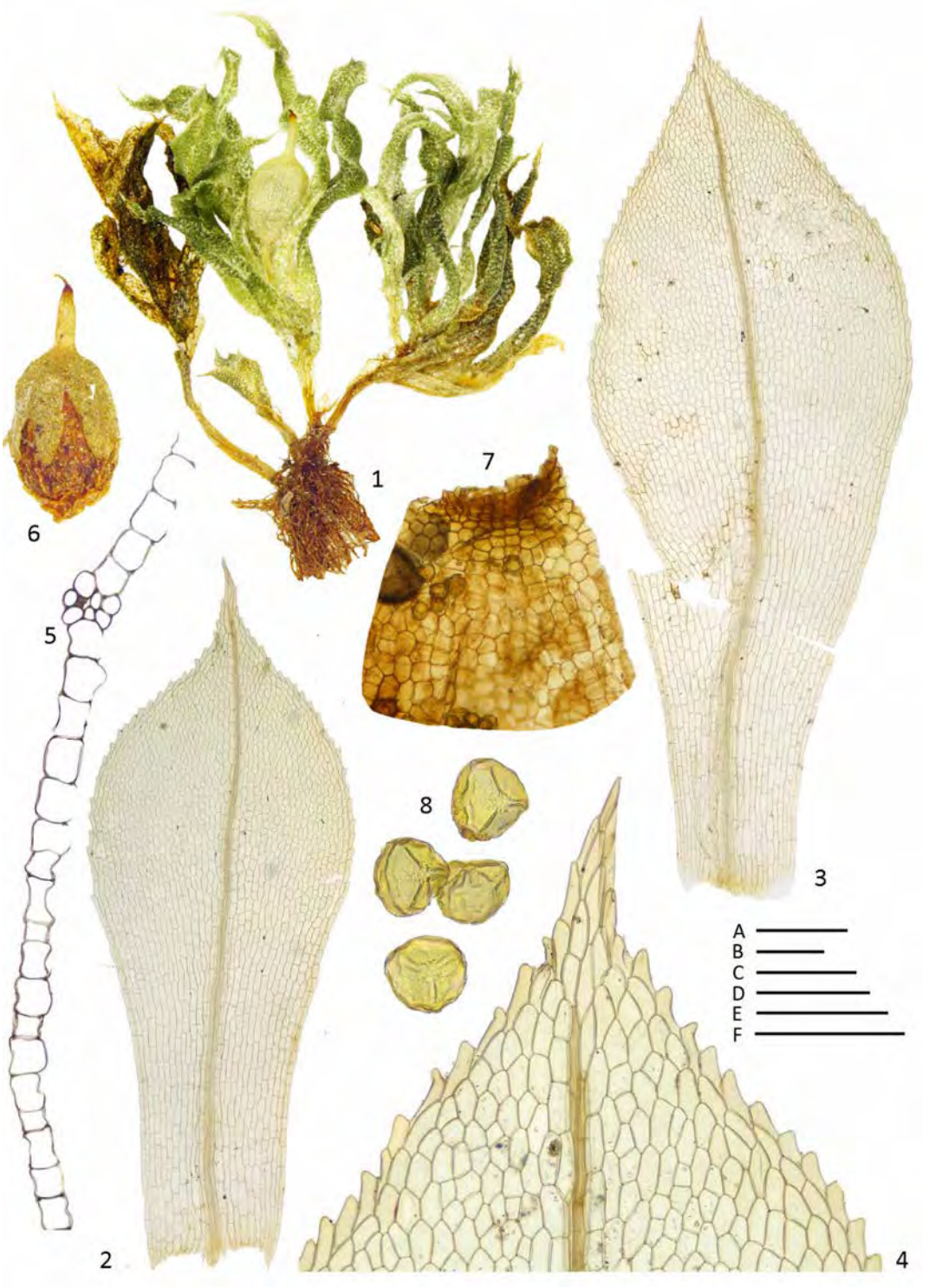

Figure 5.53: *Physcomitrellopsis africana.* 1. Habit, dry; 2, 3. Leaves; 4. Leaf apex; 5. Leaf cross-section; 6. Capsule, dry; 7. Capsule mouth & exothecial cells; 8. Spores. All from: *T.A.J. Hedderson 17577*, BOL. Scale bars: A (2, 3) = 500 µm; B (4, 7) = 100 µm; C (1) = 1 mm; D (5) = 100 µm; E (8) = 50 µm; F (6) = 1 mm.

Unplaced Nomina nuda

Entosthodon kadzianus Rehmann, nom. nud., Cape Monthly Magazine 17: 316. (1878).

6. Synthesis

This thesis provides a thorough revision of *Entosthodon sensu lato* for sub-Saharan Africa, based on all available specimens of the genus for the continent. Twenty-six species-level taxa are recognised, 6 of which are newly described. The molecular phylogenetic analysis clarifies relationships within this broadly-conceived group, as well as its relationships to other genera of Funarioideae. In the interest of meeting a monophyly criterion, *Entosthodon s.l.* is split into five genera. I also provide a temporal, biogeographic, and ecological context for the diversification of these genera, and show that the evolution of the reduced sporophyte condition that is widespread across the sub-family proceeds through correlated and sequential change in the states of a few key characters.

Inevitably, the current study is limited by time, and financial considerations. Furthermore, the investigations reported above raise a number of additional questions. Here I attempt to contextualise the key findings of the work as well as provide an agenda for further research.

6.1. Systematics and taxonomy of *Entosthodon s.l.* and the Funarioideae: where we are and what lies ahead

The phylogeny of the Funarioideae presented in Chapter 2 significantly advances our understanding of evolutionary relationships within the sub-family. For the first time, major lineages within the sub-family are resolved and the position of

Entosthodon s.l. with respect to these is now better understood. The paraphyly of *Entosthodon* as currently circumscribed had been previously suggested by Liu et al. (2012) but has been confirmed and clarified within this work. Within the Funarioideae, *Entosthodon s.l.* is shown to comprise three independent higher-level lineages. The relationships among these and to other important lineages within the sub-family, however, remain either difficult to fully resolve or else lack convincing support in favour of a single topology. Analyses in Chapter 3 reveal a high net diversification rate in *Entosthodon s.l.* supporting suspicions by Liu et al. (2012) and possibly explaining the lack of resolution among the major lineages. Of particular importance for future work is the relationship between *Amphoritheca* and *Entosthodon* (see Chapter 2, Fig 1). Alternative topologies recovered during phylogenetic analyses (not presented here) obtain a clade comprising *Amphoritheca* and *Entosthodon*, sister to the *Physcomitrium* lineage. Whether the relationship presented in Chapter 2 is robust should be confirmed using additional analyses and data. Sampling of additional species may be the best solution here because the addition of extra markers has been shown to offer little extra resolution in the Funarioideae (Liu et al., 2012). A next generation sequencing approach may hold the key to a fully resolved Funarioideae tree. A number of new methods, for example targeted sequencing, provide a cost- and time-effective way to simultaneously target hundreds of loci for many species and individuals all within a single sequencing run (Mardis, 2008). Obviously sequencing thousands of loci does not guarantee that the data will fully resolve the phylogenetic tree in question. Processes such as incomplete lineage sorting, hybridization (Beike et al., 2014; McDaniel et al., 2010), and homoplasy will continue to affect the reconstruction of evolutionary relationships (Carter, 2012; Liu et al., 2012) within the sub-family. These new approaches are thus not some holy grail of molecular systematic research but rather provide us with a best chance

of clarifying evolutionary relationships where they have long been obscured.

The biggest taxonomic task remaining for African *Entosthodon*, and perhaps for the genus globally, will be sorting out the *borbonicus* complex, which forms the crown polytomy in the phylogeny (Chapter 2, Figure 2.1). The polytomy comprises numerous species, united by their similar leaf morphology i.e. often with bordered, serrate leaf margins but with varying peristome states and capsule shapes. Within the group, *E. bonplandii*, *E. subintegrus* and *E. borbonicus* form a complex of taxa not distinguishable by morphology or DNA. All three occupy similar habitats in tropical montane cloud forests around the world suggesting that they may comprise a single species with a global distribution. The complex provides a perfect setting to test for recent gene flow between these geographically distant populations and to determine the frequency of long distance dispersal and its genetic implications for population differentiation. This can be done using coalescent methods, for example those implemented in Isolation with Migration (IM) models (Nielsen and Wakeley, 2001; Hey and Nielsen, 2004; Hey, 2010). Future work could also make use of coalescent-based approaches for determining species limits (Knowles and Carstens, 2007). These methods use a probabilistic framework to delimit species, in spite of widespread incomplete lineage sorting, by modelling the relationship between gene trees and the species history (Knowles and Carstens, 2007).

Evolution of sporophyte morphology has not occurred in a strictly linear fashion in the Funarioideae and character state reversals have occurred multiple times over the history of the group (Chapter 4). Characters relating to the sporophyte, as previously suspected, are shown to suffer from significant levels of homoplasy and this is true to a lesser extent for gametophytic characters (Chapter 4, 5). Clearly such situations are a normal, and not at all unexpected, evolutionary outcome (Collin and Miglietta, 2008; Domes et al., 2007; Galis et al., 2010; Lynch

and Wagner, 2010; Wiens, 2011). However, because the majority of taxonomically informative characters are derived from the sporophyte this has resulted in an almost complete lack of characters or combinations thereof that can be used to unambiguously circumscribe genera (Chapter 2, 4, 5). Thus, I believe the decision to circumscribe genera based mostly on molecular data is the most pragmatic solution to this problem. Given the ease of generating sequence data nowadays I do not believe this will hinder taxonomic research on the group. In many cases it may be possible to match species, with fair confidence, to ones whose phylogenetic position is already well established. For example, the species *E. cameruniae*, although not sequenced in this study, was transferred from *Funaria* to *Entosthodon* because of its overall similarity to some members of the genus. The new classification sees *Entosthodon sensu* Fife (1985), (i.e. all those species of Funarioideae that lack a compound *Funaria* type annulus, spinulose spores, isodiametric exothecial cells, and rostrate opurculae), including the monotypic genera *Funariella* and *Physcomitrellopsis* which are nested within it, reclassified to reflect evolutionarily distinct units that satisfy a monophyly criterion. Five genera are recognized - i) *Funariella*; the genus has been expanded to include additional species, ii) *Fifeobryum*; the genus is erected to accommodate species in a clade sister to *Physcomitrellopsis*, iii) *Physcomtrellopsis*; the monotypic genus is retained because of its evolutionary distinctness to other closely related species, iv) *Amphoritheca*; the generic name is resurrected to accommodate species that occur in a clade sister to the clade comprising the Physcomitrium lineage and *Entosthodon s.s.* and, v) *Entosthodon s.s.*; the genus now includes all those species sister to the Physcomitrium lineage. For the reasons discussed above no subgeneric classification is proposed for any of the genera.

The lack of informative characters has further made production of a taxonomic key for *Entosthodon s.l.* more complicated as species cannot always first

be separated by genus. Fortunately, there are sufficient unique combinations of characters states to separate all the African species of *Entosthodon s.l.* A number of synapomorphies were found that distinguish smaller clades of two to three species, e.g. the presence of a single row of ventral leaf epidermal cells in the lineage comprising *A. lindigii, A. jamesonii* and *A. productus* and the presence of a rudimentary prostome in the species pair *E. claudineae* and *E. lepervanchei*, but no characters were found that were useful for diagnosing higher-level clades within *Entosthodon s.l.* In future, the development of an electronic, interactive key will greatly aid the identification of known species and the discovery of new species. Such keys have the advantage of incorporating both images and descriptions of species that can be used in a non-linear format to identify species based on available morphological characters as well as other properties of the species such as geography and ecology.

The work discussed above resulted in the discovery and description of six new species for science (Chapter 2, 5). Three of these are from the mountainous regions of East Africa and were collected by the Hungarian bryologist T. Pócs et al. The remaining three species are from southern Africa, and were collected by various botanists over recent decades. Globally a number of areas remain relatively unexplored and may hold additional floristic novelties for *Entosthodon s.l.*. In this study specimens representing a large coverage of sub-Saharan Africa were examined, however, there were notably few from outside southern and East Africa either because of genuine low diversity in these areas or because of a lack of bryological exploration. Further exploration, particularly in arid areas where previous explorers may not have thought to visit could prove most interesting. Outside of Africa, the Middle East, Asia and non-Andean South America are areas which direly need further exploration and the species recorded from these regions should be revised.

6.1.1. A note on sexual system in *Entosthodon s.l.*

Sexuality in the *Entosthodon s.l.* has often been recorded as autoicous or rarely paroicous or polygamous (Fife, 1982) with little additional information available on sexual development in the literature. In the course of this work it became apparent that the majority of species in *Entosthodon s.l.* produce a terminal perigonium and a number of sub-perigonial, synoicous innovations (Figure 5.1) which later overtop the perigonial inflorescence. The sub-perigonial innovations seem to be protogynous, first developing archegonia and later antheridia. Antheridia are rarely observed in sub-perigonial innovations because fertilization of the archegonium appears to occur very soon after they mature, preventing later development of male sex organs. This may be the opposite of what is taking place in *Physcomitrella patens*. According to Nakosteen and Hughes (1978) the primary shoot of *Physcomitrella* can produce male and female sex organs while innovations initially produce male sex organs and later female sex organs in the same infloresence. The sexual development in *Funaria hygrometrica* and *Physcomitrium pyriforme* appears to be the same as in *Entosthodon s.l.* (Nakosteen and Hughes, 1978). Considering the diversity of sexual systems in the sub-family the Funarioideae again offer an interesting stage for future research on the topic.

6.2. Sporophytic reductions in the Funarioideae: the evolution of specialized forms

The *Funaria*-type sporophyte has been commonly considered the ancestral form within the Funarioideae while reduced morphologies were thought to represent derived states (Fife, 1985; Liu et al., 2012): the work presented here supports these early hypotheses (Chapter 4). While the dominant trend in the sub-family may be the gradual simplification of the sporophyte, it has not prevented the re-

appearance of complex character states even after they were supposedly lost – for example, the reappearance of a peristome in *Funariella* after the character was almost certainly lost early in the history of the clade (Chapter 4). Given the morphological similarity of the re-evolved ancestral states, I believe these may never have been truly lost and that silencing and reactivation of genetic pathways is the most likely explanation (Zander, 2006; Collin and Cipriani, 2003; Marshall et al., 1994).

Theory on the significance of evolutionary reductions in the moss sporophyte is well developed (e.g. During, 1979; Grout, 1908; Hedderson and Longton, 1995; Schofield, 1981; Vitt, 1981) and yet the mechanisms underlying such reductions have until now remained untested. Analyses of character state change in the Funarioideae sporophyte (Chapter 4) strongly support the presence of correlated evolution between the seta and the peristome and the capsule shape and the peristome but not directly between the seta and capsule shape. Evolutionary models of character dependence and character state change further provide a likely scenario for the order of morphological evolution in the Funarioideae sporophyte suggesting that these changes did not occur randomly. Simplification of the Funarioideae sporophyte likely began with shortening of the seta, followed by change of capsule shape and orientation and finally loss of the peristome. The ordered change of morphology provides evidence of functional interdependence between components of the moss sporophyte, suggesting that change in one character might drive changes in others. Discussion of the potential adaptive significance of these changes remains speculative in the absence of more formal tests, and the hypothesis that a relaxation or shift of ecological constraints may have lead to a loss of specialized features in favour of cheaper ones, is one that could be tested in the future (e.g. Huttunen et al., 2012).

The demonstration that a number of morphological characters are highly la-

bile in the Funarioideae is one of the most interesting results in terms of its potential implications for understanding the diversification of the sub-family. Maintenance of high morphological lability presumably increases the likelihood that the best combination of characters will evolve under a given set of environmental conditions (Kozak and Wiens, 2010). Evidence from the reconstruction of climatic niche (Chapter 3) supports a similarly high level of lability at a physiological level. The ability to quickly adapt to ecological changes would probably favour speciation, allowing species to rapidly enter and exploit new environments. Whether character lability has lead to increased rates of diversification could be tested by using a Binary (BiSSE) or Multi-State Speciation and Extinction (MuSSE) approach (see FitzJohn et al., 2009; Maddison et al., 2007). These methods use a likelihood approach to calculate the probability that a group of extant species would have evolved as observed, given a particular model of a character's effect.

6.3. Bryophyte biogeography and the diversification of *Entosthodon s.l.*

Bryophyte biogeography is characterized by taxa with broad ranges, often involving inter-continental disjunctions (Goffinet and Shaw, 2009; Delgadillo, 1993). This is supported by the situation in *Entosthodon s.l.*, which with the exception of the Polar and boreal regions, is distributed globally (Chapter 3). The ability to obtain broad geographic distributions is not limited to the bryophytes but is a feature of spore producing plants in general (Wolf et al., 2001; Muñoz et al., 2004). Thus, the production of, primarily wind dispersed, spores has allowed these plants to colonize all corners of the world. As a result of this ability, however, bryophytes tend to have significantly lower levels of endemism (Goffinet and Shaw, 2009) when compared to vascular plants and this has most likely affected global di-

versity patterns in the group. The increased dispersal ability also means that the world is effectively a smaller place for these plants. This is supported by the fact that patterns of endemism observed in angiosperms at the family level are often observed at the level of genera and species in bryophytes (Vanderpoorten and Goffinet, 2009). Thus, species-area relationships could provide a partial explanation for lower diversity in bryophytes. This is not to say that long distance dispersal is necessarily commonplace in bryophytes nor that it is a feature of all bryophyte taxa. For example, Ricciaceae are a good example of how poor dispersal ability may be linked with increased rates of diversification (Laenen et al., 2014). The Ricciaceae produce large spores that remain trapped in the thallus after the plants die, and in southern Africa the sub-family has radiated to include ca. 100 species, including many that are point-endemics or show very small ranges (Perold, 1986, 1999, 1995).

A lack of comparable biogeographic studies of African bryophytes limits possible comparisons of the distribution patterns observed in *Entosthodon s.l.*. Biogeographical patterns in African ferns (Polypodiaceae) are not unlike those of *Entosthodon s.l.*. In both groups Southern Hemisphere disjunctions are common at and above species level (Janssen et al., 2007), while Southern Hemisphere taxa with disjunctions in the Northern Hemisphere are relatively rare. The distribution patterns of bryophytes in southern Africa (Van Rooy and Van Wyk, 2010) show some congruence with White's (1983) and Linder et al's (2005) vascular plant phytochoria (see Chapter 1). However, the coarse scale of the Van Rooy and Van Wyk (2010) analyses makes further comparisons difficult. Most of the diversity and endemism of *Entosthodon s.l.* in Africa is partitioned into 3 broad phytochoria within sub-Saharan Africa (Table 6.1). The Southern African phytochorion is the most diverse of these, including 15 species of *Entosthodon s.l.*, of which 11 are endemic to the region. The next richest are the Zambezian and Madagascar-

islands regions with 7 and 8 species respectively. Both regions hold an almost equivalent number of species, and both posses 3 endemic species. These figures correspond well to those provided by Linder et al. (2005) for the vascular flora, particularly the high species diversity of the Southern African phytochorion.

Table 6.1: Diversity of *Entosthodon s.l.* species in broad African phytochria, *sensu* Linder et al. (2005), including an additional region to accommodate species from Madagascar and the western Indian Ocean islands.

Species	Southern African	Zambezian	Guineo-Congolian	Sudanian	Madagascar - islands
Amphoritheca gymnostoma	*x*				
Amphoritheca jamesonii		x	x		x
Amphoritheca lindigii					x
Entosthodon bergianus	*x*				
Entosthodon borbonicus	*x*				x
Entosthodon cameruniae			x		
Entosthodon claudineae		x			
Entosthodon curvipes		x	x		
Entosthodon heddersonii		x			
Entosthodon lepervanchei					x
Entosthodon limbatus	*x*				x
Entosthodon pertenellus		x			x
Entosthodon pocsii		x			
Entosthodon rhomboideus	*x*				
Entosthodon zygolimbatus	*x*	x			
Funariella campylopodioides	*x*				
Funariella chevalierii				x	
Funariella clavata	*x*				
Funariella longicollis	*x*				x
Funariella mayottensis					x
Funariella sebapala	*x*				
Funariella spathulata	*x*				
Funariella succuleata	*x*				
Funariella sulcata	*x*				
Funariella urceolata	*x*				
Physcomitrellopsis africana	*x*				
Total no. of species	**15**	**7**	**3**	**1**	**8**
Species restricted to phytochorion	**11**	**3**	**1**	**1**	**3**
African endemics	**15**	**6**	**2**	**1**	**6**
Percent endemic to Africa	**100**	**86**	**67**	**100**	**75**

A closer look at the southern African species shows that the highest diversity is in the Grassland and Savanna biomes (Table 6.2), reflecting results from Chapter 3. The grassland biome in particular also has the highest number of endemic species. Species richness and endemism among the other 6 biomes is relatively much lower and fairly invariable. Clearly, at this scale diversity patterns do not

reflect those seen in angiosperms where the Fynbos biome is renowned for its incredible species richness (Linder et al., 2005). Partial congruence of phytogeographic patterns between the vascular flora and those observed in *Entosthodon s.l.* support the premise that bryophytes may respond similarly to factors determining richness and endemism, albeit often at different taxonomic scales.

Table 6.2: Diversity of southern African species of *Entosthodon s.l.* per biome. Biomes according to the South African National Biodiversity Institute (SANBI).

Species	Fynbos	Succulent Karoo	Nama-Karoo	Grassland	Desert	Savanna	Albany thicket	Forest
Amphoritheca gymnostoma				x				
Entosthodon bergianus	x							
Entosthodon borbonicus				x		x		
Entosthodon limbatus	x			x		x		
Entosthodon rhomboideus			x		x			
Entosthodon zygolimbatus				x				
Funariella campylopodioides			x	x		x	x	
Funariella clavata	x	x						
Funariella longicollis						x		
Funariella sebapala				x				
Funariella spathulata		x	x					
Funariella succuleata				x				
Funariella sulcata					x			
Funariella urceolata				x		x	x	x
Physcomitrellopsis africana								x
Total no. of species	3	2	3	8	2	5	2	2
No. of species endemic	1	0	0	4	1	1	0	1
Percent species endemic	33	0	0	50	50	20	0	50

The general lack of fossil bryophytes has led to the use of alternative methods for the calibration of phylogenetic trees (Villarreal and Renner, 2014). These methods include the use of biogeographic events, rates of molecular substitution and secondary calibrations. Bryophyte dating studies have thus far used one or a combination of calibration methods which may include the use of any available fossil evidence and subsequent cross-validation of these results to determine whether divergence estimates are comparable. The use of secondary calibrations has been advised against because it is prone to propagating further error in the

analysis (Shaul and Graur, 2002; Graur and Martin, 2004). The use of a secondary calibration for the Funarioideae yielded divergence estimates with much wider probability intervals than the alternative methods (Chapter 2), offering little support for this method. Rather, the use of biogeographic events, which have, however, met much criticism (Heads, 2011), and a known substitution rate may be better alternatives for time calibrating trees at least in the Funarioideae.

The high net diversification rate observed in *Entosthodon s.l.* adds to a growing number of studies (Laenen et al., 2014; Wall, 2005; Huttunen et al., 2008) showing that rapid radiations have occurred in bryophyte taxa within the recent past, refuting older beliefs that bryophytes represent unchanging evolutionary fossils with slow rates of molecular evolution (Goffinet and Shaw, 2009).

6.4. Final Thoughts

The most significant contribution of this thesis is certainly the taxonomic revision. With this now complete, we know that 26 species of *Entosthodon s.l.* are present in sub-Saharan Africa, species identities and distributions are significantly better understood and for the first time a key and plates are provided for all species known from the region. This should facilitate further study of the group and is likely to spur the discovery of additional taxa with increased collecting effort.

From a personal perspective, the undertaking of a taxonomic revision immensely aided not only the interpretation of phylogenetic relationships, but also the formulation of hypotheses of potential relationships. In particular, the examination of multiple specimens affords the taxonomist an ability to differentiate between characters that are uninformative and those that may be of evolutionary significance. Revising the African *Entosthodon s.l.* has afforded me an intimate understanding of these fascinating plants, one that I hope to develop further in

coming years.

The step towards a more in-depth understanding of sporophytic reductions in mosses is only the first step to fully understanding the evolution and adaptive significance of the moss sporophyte. The next step will involve establishing environmental correlates of character state change (e.g. Huttunen et al., 2012) and determining whether these are linked with shifts in diversification rate (e.g. Onstein et al., 2014).

Finally, work on the biogeography of *Entosthodon s.l.* has contributed towards a general understanding of bryophyte distributions and provides the first study of its kind for Africa. The addition of similar studies and distillation of the available literature will help to develop a more comprehensive overview and understanding of biogeographic patterns in African bryophytes.

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A. Appendix

Table A.1: Voucher information and GenBank accession numbers for taxa sequenced in this study. Except for Genbank accessions, sequences are newly generated.

Name in phylogeny	Collection number	Locality	Herbarium	atpB-rbcL	psbA-trnH	rps4	trnL-F
Aphanorrhegma serratum 1	BG-NC	USA	Duke	JN089196	JN089041	JN088967	JN088933
Aphanorrhegma serratum 2	Buck 49500	USA	NYBG	JN089197	JN089042	JN088968	JN088934
Bryobeckettia bartlettii	Beveridge 564868	New Zealand	CHR	JN089199	JN089044	JN088969	JN088936
Entosthodon abramovae	Fedosov #10-2-8	Russia	CONN	x	x	x	x
Entosthodon americanus	Goffinet 4347	Canada	CONN	x	x	x	x
Entosthodon apophysatus 1	Vitt 27234	Australia	ALTA	x	x	x	x
Entosthodon apophysatus 2	Bellolio 31919	Chile	CONN	JN089206	JN089051	JN088972	JN088939
Entosthodon attenuatus 1	Long 38559	Ireland	CONN	x	x	x	x
Entosthodon attenuatus 2	Shevock 23875	USA	CAL	x	x	x	x
Entosthodon attenuatus 3	Tour 9765	USA		x	x	x	x
Entosthodon balansae	Lozano and Flores 2778	Bolivia	MO	x	x	x	x
Entosthodon bergianus 1	Hedderson 15276	South Africa	BOL	x	x	x	x
Entosthodon bergianus 2	Wilding 208	South Africa	BOL	x	x	x	x
Entosthodon bergianus 3	HBCT 301c	South Africa	BOL	x	x	x	x
Entosthodon bonplandii 1	Goffinet 6326	Mexico	CONN	JN089207	JN089052	AF223042	AF229899
Entosthodon bonplandii 2	*Lozan and Mendoza et al 2885*	Bolivia	MO	x	x	x	x
Entosthodon borbonicus 1	Kis 9465/DA	Madagascar	BOL	x	x	-	-
Entosthodon borbonicus 2	Wilding 37a	Reunion	BOL	x	x	x	x
Entosthodon borbonicus 3	Hedderson 16301	Reunion	BOL	x	x	x	x
Entosthodon campylopodioides 1	Kroon 16309	South Africa	PRE	x	x	x	x
Entosthodon campylopodioides 2	Van Rooy 2404	South Africa	PRE	x	x	x	x
Entosthodon campylopodioides 3	Van Rooy 2456	South Africa	PRE	x	x	x	x
Entosthodon claudinae 1	Pócs Ochyra & Bednarek-Ochyra 88152/BH	Tanzania	BOL	x	x	x	x
Entosthodon claudinae 2	Pócs 88094/BH	Tanzania	BOL	x	x	x	x
Entosthodon claudinae 3	Pócs 88093/D	Tanzania	BOL	x	x	-	x
Entosthodon clavatus South Africa 1	Hedderson 14316	South Africa	BOL	x	x	x	x
Entosthodon clavatus South Africa 2	Hedderson 16877	South Africa	BOL	x	x	x	x
Entosthodon clavatus South Africa 3	Hedderson 16864	South Africa	BOL	x	x	x	x
Entosthodon convexus	Herbarium no., 53810	Spain	BCB	x	x	x	x

Table A.1: (continued).

Name in phylogeny	Collection number	Locality	Herbarium	atpB-rbcL	psbA-trnH	rps4	trnL-F
Entosthodon curvipes 1	Pócs?	Kenya	CONN	x	x	x	x
Entosthodon curvipes 2	Pócs & Szabo 9218/DN	Tanzania	BOL	x	x	x	x
Entosthodon dixonii	Van Rooy 621	South Africa	BOL	x	x	x	x
Entosthodon drummondii	Shaw s.n.	USA	DUKE	JN089208	JN089053	AF306961	JN088940
Entosthodon duriaei 1	Ros & Werner	Spain	MUB	x	x	x	x
Entosthodon duriaei 2	Ros & Alendi 100407	Spain		x	x	x	x
Entosthodon handelii	MW#10-2-6	Russia	CONN	x	x	x	x
Entosthodon hungaricus 1	Frahm 70325	Austria		x	x	x	x
Entosthodon hungaricus 2	Suragina S.A.	Russia	CONN	x	x	x	x
Entosthodon hungaricus 3	R.M. Ros & O. Werner	Spain	MUB	x	x	x	x
Entosthodon jamesonii 1	Hedderson 15811	Reunion	BOL	x	x	x	x
Entosthodon jamesonii 2	Pócs , Ochyra & Bednarek-Ochyra 88152/BJ	Tanzania	BOL	x	x	x	x
Entosthodon laevis 1	Goffinet 5601	Chile	CONN	JN089210	JN089055	AY908156	AF229900
Entosthodon laevis 2	Ireland & Bellolio 31968	Chile	NYBG	x	x	x	x
Entosthodon laxus 1	Nuck 56982	Chile	NYBG	x	x	x	x
Entosthodon laxus 2	Fife 12133	New Zealand	CHR	JN089211	JN089056	JN088974	JN088942
Entosthodon laxus 3	Griffin PV-1050	Venezuela	PRE	x	x	-	x
Entosthodon lepervanchei 1	Ah-Peng & Hedderson R384.17	Reunion	BOL	x	x	x	x
Entosthodon lepervanchei 2	Szabo 9640/CD	Reunion	BOL	x	x	x	x
Entosthodon limbatus 1	Wilding 172	South Africa	BOL	x	x	x	x
Entosthodon limbatus 2	Hedderson 15505	South Africa	BOL	x	x	x	x
Entosthodon limbatus 3	Wilding 218	South Africa	BOL	x	x	x	x
Entosthodon limbatus 4	Strasberg & Warren REU 05367	Reunion	BOL	x	x	-	x
Entosthodon lindigii	Hedderson 16805	South Africa	BOL	x	x	-	x
Entosthodon mouretii	Herbarium no., 50005	Spain	BCB	x	x	x	x
Entosthodon muhlenbergii	Luth 5365	Greece	Luth	JN089214	JN089059	JN088977	JN088945
Entosthodon obtusifolius 1	Villarreal 1211	Mexico	CONN	x	x	x	x
Entosthodon obtusifolius 2	Ireland and Bellolio 31874 (MO)	Chile	MO	x	x	x	x
Entosthodon obtusus 1	Holyoak 04-87	Ireland	CONN	JN089213	JN089058	JN088976	JN088944
Entosthodon obtusus 2	Holyoak 04-87	Ireland	NYBG	x	x	x	x

Table A.1: (continued).

Name in phylogeny	Collection number	Locality	Herbarium	atpB-rbcL	psbA-trnH	rps4	trnL-F
Entosthodon pertenellus 1	Hedderson 17491	Malawi	BOL	x	x	x	x
Entosthodon pertenellus 2	Pócs 9159/AL	Grande Comore	BOL	x	x	-	x
Entosthodon pertenellus 3	Wilding 151	Reunion	BOL	x	x	x	x
Entosthodon planoconvexus	Shevock 26542	USA	CAL	x	x	x	x
Entosthodon pocsii 1	Iversen, Persson, Petterson & Pócs 87145/N	Tanzania	BOL	x	x	-	x
Entosthodon pocsii 2	Iversen, Persson, Petterson, Pócs 87145/D	Tanzania	BOL	x	x	x	x
Entosthodon pocsii 3	Pócs , Harrison & Mushy 90130/U,V	Tanzania	BOL	x	x	-	-
Entosthodon productus				x	x	x	x
Entosthodon pulchellus 1	Ros & Pisa	Spain	MUB	x	x	x	x
Entosthodon pulchellus 2	Ros, Werner & Magdy	Spain	MUB	x	x	x	x
Entosthodon radians	JR Shevock 31458	Australia	BOL	-	-	x	x
Entosthodon rhomboideus 1	Mannheimer 246	Namibia	PRE	x	x	x	x
Entosthodon rhomboideus 2	Volk 00481	Namibia	PRE	x	x	-	x
Entosthodon rhomboideus 3	Hedderson 13203	South Africa	BOL	x	x	x	x
Entosthodon schimperi	Long 38230 & Runasinghe	Spain	CONN	x	x	x	x
Entosthodon sebapala	Van Rooy 3564	Lesotho	PRE	x	x	-	x
Entosthodon serratus	Frank & Robert 13109	USA	WIS	JN089215	JN089060	JN088978	JN088946
Entosthodon smithhurstii	Downing, Osborne, & Downing (NSW 72001798)	Australia	CONN	x	x	x	x
Entosthodon spathulatus 1	Goffinet 10200	South Africa	CONN	x	x	x	x
Entosthodon spathulatus 2	Hedderson 16478	South Africa	BOL	x	x	x	x
Entosthodon subintegrus	Wilding 224	Hawaii	BOL	-	-	-	x
Entosthodon urceolatus 1	Wilding 245	South Africa	BOL	x	x	x	x
Funaria arctica 1	LaFarge-England 13433	Canada	ALTA	x	x	x	x
Funaria arctica 2	LaFarge-England 13722	Canada	ALTA	x	x	x	x
Funaria chilensis	Ireland and Bellolio 31954	Chile	MO	x	x	x	x
Funaria costesii 1	García 2996	Chile	CONN	x	x	x	x
Funaria costesii 2	Mahu and Mahu 13305	Chile	MO	x	x	-	x
Funaria flavicans 1	Goffinet 4798	USA	CONN	x	x	x	x

Table A.1: (continued).

Name in phylogeny	Collection number	Locality	Herbarium	atpB-rbcL	psbA-trnH	rps4	trnL-F
Funaria flavicans 2	Goffinet 9345	USA	CONN	JN089216	JN089061	JN088979	JN088947
Funaria hygrometrica 1	Wang 54398	China	PE	x	x	x	x
Funaria hygrometrica 2	Goffinet 5576	Chile	CONN	DQ397164	JN089062	JN088980	JN088948
Funaria hygrometrica 3	Mai Taha	Egypt	CONN	x	x	x	x
Funaria hygrometrica var calvescens 2	Lozano 2863	Bolivia	MO	x	x	x	x
Funaria hygrometrica var calvescens 3	Pócs 8267	Rwanda	CONN	x	x	x	x
Funaria hygromterica var calvescens 1	Wilding 34b	Réunion	CONN	x	x	x	x
Funaria microstoma 1	Miehe & Liu & Sonamco	China		x	x	x	x
Funaria microstoma 2	Hedderson 2602	Canada	MO	x	x	x	x
Funaria succuleata 1	Van Rooy 2703	South Africa	PRE	x	x	-	x
Funaria succuleata 2	Van Rooy 3289	Lesotho	PRE	x	x	x	x
Funaria succuleata 3	Van Rooy 3369	Lesotho	PRE	x	x	x	x
Funariella curviseta 1	Ros & Werner 26-3-2006	Spain	MUB	JN089218	JN089064	JN088982	JN088950
Funariella curviseta 2	Long 38236 Runasinghe	Spain	CONN	x	x	x	x
Funariella curviseta 3	Ros & Werner 15/1/2006	Spain		x	x	x	x
Loiseaubryum nutans 1	Kornas 5	Nigeria		x	x	x	x
Loiseaubryum nutans 2	Kornas 5	Nigeria	PC	x	x	x	x
Physcomitrella magdalenae 1	Hylander 5631	Ethiopia	CONN	x	x	x	x
Physcomitrella magdalenae 2	Buchbender RWA-VB-0107	Rwanda	IMSC	JN089226	JN089072	JN088988	JN088956
Physcomitrella magdalenae 3	RWA-VB-0107 ecotype E2	Rwanda	IMSC	x	x	x	x
Physcomitrella patens 1	cult. from Schaefer WT-GB			x	x	x	x
Physcomitrella patens 2	Spribille	Canada	CONN	x	x	x	x
Physcomitrella patens 3	Withehouse 1962	UK	IMSC	JN089228	JN089074	AP005672	JN088958
Physcomitrella readeri 1	Entrer 17545	USA	MO	JN089229	JN089075	JN088990	JN088959
Physcomitrella readeri 2	Shevock 32591	USA	CONN	x	x	x	x
Physcomitrellopsis africana 1	Goffinet 10316	South Africa	CONN	x	x	x	x
Physcomitrellopsis africana 2	Goffinet 10330	South Africa	CONN	x	x	x	x
Physcomitrium collenchymatum	Budke 185		CONN	x	x	x	x
Physcomitrium coorgense 1	Vanderpoorten	Laos		x	x	x	x
Physcomitrium coorgense 2	Vanderpoorten THAI 1010	Thailand	LG	x	x	x	x
Physcomitrium eurystomum	Frahm 10979	Germany		x	x	x	x

Table A.1: (continued).

Name in phylogeny	Collection number	Locality	Herbarium	atpB-rbcL	psbA-trnH	rps4	trnL-F
Physcomitrium hookeri 1	Budke 195	USA	CONN	x	x	x	x
Physcomitrium hookeri 2	Budke 177B	USA	CONN	x	x	x	x
Physcomitrium immersum 1	Shaw 4827	USA	DUKE	JN089231	JN089077	JN088992	JN088961
Physcomitrium immersum 2	Christy 8505-1	USA	DUKE	JN089230	JN089076	JN088991	JN088960
Physcomitrium japonicum 1	Akiyama 22212	Japan	CONN	x	x	x	x
Physcomitrium japonicum 2	Tamura 2004	Japan	CONN	x	x	x	x
Physcomitrium lorentzii	Goffinet 5348	Chile	DUKE	JN089232	JN089078	AF223046	AF229903
Physcomitrium pyriforme 1	Budke 177A		CONN	x	x	x	x
Physcomitrium pyriforme 2	Goffinet 4737	USA	CONN	JN089233	JN089079	JN088993	JN088962
Physcomitrium pyriforme 3	Goffinet 9346	USA	CONN	x	x	x	x
Physcomitrium pyriforme 4	Goffinet 9204		CONN	x	x	x	x
Physcomitrium pyriforme 5	Goffinet 9276	USA	CONN	JN089234	JN089080	JN088994	JN088963
Physcomitrium sp 1	Goffinet et al. 9937	China	CONN	x	x	x	x
Physcomitrium sp 2	Goffinet et al. 9952	China	CONN	x	x	x	x
Physcomitrium sp 3	Goffinet 9811	China	CONN	x	x	x	x
Physcomitrium sp 4	Goffinet 9878	China	CONN	x	x	x	x
Physcomitrium sp 5	Goffinet 9782	China	CONN	x	x	x	x
Physcomitrium sp 6	Goffinet 9783	China	CONN	x	x	x	x
Physcomitrium sp 7	Frahm 20.4.94	Germany	CONN	JN089209	JN089054	JN088973	JN088941
Physcomitrium spathulatum	Goffinet 10312	South Africa	CONN	x	x	x	x
Physcomitrium subspathulatum	De Sloover 18754	Rwanda	BOL	x	x	-	x
Physcomitrium subsphaericum	Villarreal 1218	Mexico	CONN	x	x	x	x

Table A.2: Binary coded states for climatic niche and ecozone

Species name	Climatic niche	Ecozone
Amphoritheca_abramovae	A	F
Amphoritheca_americanus	D	E
Amphoritheca_duriaei	B	F
Amphoritheca_jamesonii	E	ABCD
Amphoritheca_lindigii	E	AC
Amphoritheca_producta	D	B
Amphoritheca_pulchella	B	F
Entosthodon_attenuatus	D	EF
Entosthodon_bergianus	A	B
Entosthodon_bonplandii	C	E
Entosthodon_borbonicus	A	E
Entosthodon_claudineae	A	E
Entosthodon_convexus	F	B
Entosthodon_drummondii	E	D
Entosthodon_handelii	F	A
Entosthodon_laxus	BC	E
Entosthodon_lepervanchei	A	E
Entosthodon_limbatus	A	ABE
Entosthodon_mouretii	F	B
Entosthodon_muhlenbergii	BF	D
Entosthodon_obtusifolius	C	E
Entosthodon_obtusus	F	D
Entosthodon_perlaxus	A	E
Entosthodon_pertenellus	A	E
Entosthodon_planoconvexus	E	D
Entosthodon_pocsii	A	E
Entosthodon_radians	BC	E
Entosthodon_rhomboideus	A	A
Entosthodon_schimperi	F	B
Entosthodon_serratus	E	D
Entosthodon_subintegrus	E	E
Fifeobryum_balansae	C	B
Fifeobryum_longicollis	A	A
Fifeobryum_smithhurstii	B	B
Funariella_apophysata	BC	B
Funariella_campylopodioides	A	A
Funariella_chilensis	A	B
Funariella_clavata	C	B
Funariella_curviseta	F	B
Funariella_laevis	A	E
Funariella_sebapala	A	A
Funariella_spathulata	A	B
Funariella_succuleata	A	A
Funariella_urceolata	A	A
Physcomitrellopsis_africana	A	A

Key	
Climatic niche	
Temperate steppe	A
Mediterranean	B
Temperate oceanic	D
Tropical	E
Ecozone	
Afrotropic	A
Australasia	B
Neotropic	C
Indomalaya	D
Nearctic	E
Palearctic	F

Table A.3: Binary coded morphological characters of the sporophyte

Species name	**Limbidium** (present=1, absent=0)	**Peristome** (present=1, absent=0)	**Capsule radially symmetric** (present=1, absent=0)	**Sporophyte exserted** (present=1, absent=0)	**Seta > 1 cm** (present=1, absent=0)
Amphoritheca_abramovae	0	1	1	1	1
Amphoritheca_americanus	0	1	0	1	0
Amphoritheca_duriaei	0	1	1	1	0
Amphoritheca_duriaei	0	1	0	1	0
Amphoritheca_jamesonii	0	1	1	1	1
Amphoritheca_lindigii	0	1	1	1	0
Amphoritheca_producta	0	0	1	1	0
Amphoritheca_pulchella	0	1	0	1	0
Aphanorrhegma_serratum	0	0	1	0	0
Bryobeckettia_bartlettii	0	0	1	1	0
Entosthodon_attenuatus	0	1	1	1	1
Entosthodon_bergianus	0	1	1	1	0
Entosthodon_bonplandii	1	1	1	1	1
Entosthodon_borbonicus	1	0	1	1	1
Entosthodon_borbonicus	1	0	1	1	1
Entosthodon_claudineae	0	1	0	1	0
Entosthodon_commutatum	0	1	1	1	0
Entosthodon_convexus	0	1	0	1	1
Entosthodon_convexus	0	1	0	1	0
Entosthodon_drummondii	0	1	1	1	1
Entosthodon_handelii	0	1	0	1	1
Entosthodon_laxus	0	1	1	1	1
Entosthodon_lepervanchei	1	1	0	1	1
Entosthodon_limbatus	1	1	1	1	1
Entosthodon_limbatus	1	0	1	1	0
Entosthodon_limbatus	1	0	1	1	1
Entosthodon_muhlenbergii	0	1	0	1	1
Entosthodon_obtusifolius	0	1	1	1	1
Entosthodon_obtusifolius	0	1	1	1	1
Entosthodon_obtusus	1	0	1	1	0
Entosthodon_perlaxus	0	1	0	1	0
Entosthodon_pertenellus	0	0	1	1	0
Entosthodon_planoconvexus	0	1	1	1	0
Entosthodon_pocsii	0	1	1	1	0
Entosthodon_radians	1	1	0	1	0
Entosthodon_rhomboideus	0	1	1	1	0
Entosthodon_serratus	0	1	0	1	1
Entosthodon_sp	1	0	1	1	1
Entosthodon_sp_Tanzania_SP37	0	1	0	1	0
Entosthodon_sp8	1	1	1	1	0
Entosthodon_subintegrus	1	1	1	1	1
Fifeobryum longicollis	0	0	1	1	0
Fifeobryum_balansae	0	0	1	1	0

Table A.3: (continued).

Species name	**Limbidium** (present=1, absent=0)	**Peristome** (present=1, absent=0)	**Capsule radially symmetric** (present=1, absent=0)	**Sporophyte exserted** (present=1, absent=0)	**Seta > 1 cm** (present=1, absent=0)
Fifeobryum_smithhurstii	0	0	1	1	0
Funaria_arctica	0	1	0	1	0
Funaria_calvescens	1	1	0	1	1
Funaria_flavicans	0	1	0	1	1
Funaria_hygrometrica	1	1	0	1	1
Funaria_microstoma	0	1	0	1	1
Funariella_apophysata	0	0	1	1	0
Funariella_chilensis	0	0	1	1	0
Funariella_campylopodioides	0	0	1	1	0
Funariella_clavata	0	0	1	1	0
Funariella_curviseta	0	0	0	1	0
Funariella_laevis	0	1	0	1	0
Funariella_sebapala	0	1	1	1	0
Funariella_spathulata	0	1	0	1	0
Funariella_succuleata	0	1	0	1	0
Funariella_urceolata	0	0	1	1	0
Loiseaubryum_ephemeroides	0	0	1	1	0
Physcomitrella_magdalenae	0	0	1	0	0
Physcomitrella_patens	0	0	1	0	0
Physcomitrella_readeri	0	0	1	0	0
Physcomitrellopsis_africana	0	0	1	0	0
Physcomitrium_coorgense	1	0	1	1	0
Physcomitrium_eurystomum	1	0	1	1	0
Physcomitrium_hookeri	0	0	1	1	0
Physcomitrium_hungaricus	0	1	1	1	0
Physcomitrium_immersum	1	0	1	0	0
Physcomitrium_japonicum	1	0	1	1	0
Physcomitrium_lorentzii	1	0	1	0	0
Physcomitrium_pyriforme	1	0	1	1	1
Physcomitrium_subspathulatum	1	0	1	1	0
Physcomitrium_subsphaericum	1	0	1	1	0